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Systematics of *Laccaria* (Agaricales) in the Continental United States and Canada, with Discussions on Extralimital Taxa and Descriptions of Extant Types

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Back cover: Laccaria longipes

This work is dedicated to Nils Fries and Rolf Singer, two modern pioneers of mycology who set the stage for this study.

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I have already mentioned the invaluable technical help that my wife Betty Strack provided to this project, but this was only a fraction of her contribution. Simply put, Betty—thanks for everything!

G.M.M.

Systematics of *Laccaria* (Agaricales) in the Continental United States and Canada, with Discussions on Extralimital Taxa and Descriptions of Extant Types

Gregory M. Mueller

Abstract

The genus *Laccaria* comprises an important part of the North American mycota north of Mexico. Nineteen species are recognized from the study area. *Laccaria laccata* is further divided into two varieties. Discussions regarding the distribution, presumed ectomycorrhizal hosts, and biology of these taxa are provided along with data on select extralimital taxa. In addition to an examination of North American material, an attempt was made to examine all extant type specimens. Descriptions of these collections are offered. To facilitate further work on the genus, a tentative key to the world taxa of *Laccaria* is presented.

Extensive collecting was undertaken in much of the continental United States and southern Canada. Comparative material was collected in Costa Rica, South America, and Sweden. Data were obtained on basidioma and somatic culture mat morphology, intercollection pairing reactions, and restriction fragment length polymorphisms of mtDNA and rDNA. Cytological data and in vitro ectomycorrhizal synthesis data were also obtained and used to further characterize the genus. Taxa were delimited so that they are presumably monophyletic and are diagnosable by a unique combination of character states, either morphological or molecular. Data from intercollection pairings were used in conjunction with other data sets and did not outweigh information from the other analyses. Results of cladistic analyses were concordant with the hypothesis that *Laccaria* is a monophyletic assemblage of taxa with at least one synapomorphy (echinulate basidiospores with echinulae formed by perpendicular microtubules) supporting its monophyly. However, it was not possible to develop a fully resolved, robust hypothesis of phylogeny within the genus because of a paucity of characters, inability to polarize some of these characters, and problems in choosing appropriate outgroup(s). As expected, there was a high degree of homoplasy detected within the employed data set, and it will be necessary to utilize either extensive restriction site mapping or sequencing of selected macromolecules to develop a robust hypothesis of phylogenetic relationships within this genus. Although synapomorphies were not found to support the recognition of sections in the genus, two metasections, *Laccaria* and *Amethystina,* are recognized for logistic reasons and to provide a hypothesis to be tested during future analyses.

Introduction

Laccaria Berkeley & Broome is a cosmopolitan genus of mushrooms (Agaricales) collected frequently throughout North America. Its taxa make up a sizable part of the world's mycota and have been reported from every continent except Antarctica.

Individuals of most *Laccaria* species have been reported to form ectomycorrhizal associations with numerous tree species, including many that are economically important in North America (e.g., species of *Quercus* and other Fagaceae, many species of *Pinus, Pseudotsuga menziesii* (Mirb.) Franco, and *Tsuga heterophylla* (Raf.) Sarg.) (Trappe, 1962).

Singer and Moser (1965) and Watling (1977) have reported that some taxa of *Laccaria* can act as pioneer species. Other studies have supported this contention by reporting that basidiomata of at least some *Laccaria* are frequently found in recently disturbed sites and young forest stands but not in mature forests (e.g., Danielson, 1984; Dighton & Mason, 1985; Dighton et al., 1986). Thus *Laccaria,* at least in some situations, may play an important role in primary and secondary succession.

Because of the relative ease with which some species of *Laccaria* can be manipulated in the laboratory, several taxa, including *L. bicolor* (Maire) Orton, *L. laccata* (Scop.: Fr.) Cooke, and *L. proxima* (Boud.) Pat., are being used actively in applied and basic research on ectomycorrhizae (see Kropp & Langlois, 1990). *Laccaria* has also proved useful in studies on the biology of fungi that form ectomycorrhizae (e.g., Fries, 1983a; Fries & Mueller, 1984; Kropp & Fortin, 1988; Armstrong et al., 1989; Barrett et al., 1989, 1990; Doudrick & Anderson, 1989; Gardes et al., 1990, 1991a,b; Mueller, 1991c; Mueller & Gardes, 1991).

Stabilization of the classification of *Laccaria,* therefore, would have applied implications because of the ecological and potential economic importance of many of its taxa, in addition to adding to our basic knowledge of fungi that form ectomycorrhizae.

Although most modern systematists consider *Laccaria* to be an autonomous genus, easily segregated from other members of the family Tricholomataceae (Singer, 1986), delimitation of infrageneric taxa is difficult in many instances. Much of this problem is due to the relative morphological simplicity of its taxa, which provides few suites of systematically informative characters, coupled with a high degree of phenetic plasticity within certain *Laccaria* taxa, especially those that have an apparently wide geographic range. Continuing nomenclatural confusion has exacerbated this problem.

A large discrepancy exists in the number of recognized taxa in the genus for these reasons. Although nearly 100 species epithets have been used for *Laccaria* worldwide, Singer (1986) recognized only 18 clearly defined species, while McNabb (1972) indicated that there may be as many as 43 species worldwide. There also has been much confusion concerning the circumscription of several taxa, and classification in this genus remains in a state of flux (e.g., Singer, 1967, 1977, 1986; Bon, 1983; Moser, 1983; Clémençon, 1984; Ballero & Contu, 1987, 1989; Mueller, 1991a).

This study was undertaken in an attempt to resolve systematic and nomenclatural problems, to determine species composition and distribution for the genus *Laccaria* in North America north of Mexico, and to add to our knowledge of its biology. Because of the problems stated above, it was necessary to examine extralimital taxa as well as all available extant type collections, to designate lectotypes, neotypes, or representative specimens when applicable, and to examine critically characters from various stages of the life cycle. In addition to morphological characters of basidiomata and somatic culture mats, data from intra- and interstock pairing analyses, restriction fragment length polymorphisms of mitochondrial and ribosomal DNA, cytological studies, and in vitro ectomycorrhizal synthesis attempts were incorporated into this multifaceted study.

Taxa were delimited so that they are presumably monophyletic and are diagnosable by a unique combination of character states. Attempts were made to develop a classification for the genus that reflects the evolutionary history of the group.

This monograph, the results of over 12 years of study, synthesizes new and previously published data (Mueller & Sundberg, 1981; Fries & Mueller, 1984; Mueller, 1984, 1985, 1987, 1991a,b,c; Mueller & Vellinga, 1986, 1990; Vellinga & Mueller, 1987; Gardes et al., 1990,1991a,b; Mueller & Gardes, 1991).

Taxonomic and Nomenclatural History

Europe and Other Extralimital Areas

The name *Laccaria* was first proposed by Berkeley and Broome in 1883 to accommodate species of *Agaricus* subgenus *Clitocybe* that produced globose basidiospores that often formed a white pulverulescence on the thick, attached lamellae. Proposed for transfer to the new genus were *Agaricus laccatus* Scopoli, *A. bellus* Persoon, and several unnamed species from Ceylon and Europe. No

new combinations were made until the following year, however, when Cooke (1884) formally transferred eight species to the genus.

Over the intervening century, the presence of clamp connections and echinulate, multinucleate basidiospores have become important characters in the modern generic concept of *Laccaria* (Kühner, 1980, 1984; Singer, 1986).

The pre-Friesian history of the genus can be summarized as follows. Scopoli (1772), describing fungi from the Tyrol of southern Austria, was the first to use the binomial *A. laccatus* for a member of the eventual genus *Laccaria*. Two more species, *A. amethystinus* and *A. farinaceus,* were described in 1778 by Hudson from the environs of London (Hudson, 1798). Hudson placed *A. laccatus* in synonymy with *A. farinaceus,* and thus *A. farinaceus* is a superfluous name. *Agaricus tortilis* was described from Halifax by Bolton (1788). Finally, Persoon (1801) named *A. bellus* and two varieties of *A. farinaceus*: var. *rosellus* and var. *tortilis.*

Fries (1821) placed *A. laccatus* and *A. bellus* in tribe VIII *Clitocybe,* subtribe 4 *Oseypii.* He further divided *A. laccatus* into variety "a" ("Pileo rufo 1. carneo, sicco subochraceo") and variety "b" ("Pileo amethystino, sicco canescente"). Additionally, he listed *A. tortilis* and *A. pachyphyllus* Fries (1815) as species that needed to be further examined.

Between 1821 and 1884, a number of workers described new species destined later to be incorporated in *Laccaria* (e.g., Fries, 1836–1838, 1874; Berkeley, 1845, 1856; Montagne, 1856; Berkeley & Curtis, 1859; Berkeley & Broome, 1871; Ellis, 1874; Karsten, 1876; Spegazzini, 1880; Boudier, 1881).

The genus *Russuliopsis* was proposed by Schroeter (1889) for all the taxa previously included in *Laccaria.* Because *Laccaria* and its included taxa were validly published, *Russuliopsis* is a later typonym and thus a superfluous name.

Laccaria was recognized by both Fayod (1889) and Patouillard (1900) in their attempts to develop a more natural classification system for the Hymenomycetes. Peck (1912) was the first worker in the United States to recognize the genus and one of the first in the world to publish a paper exclusively on the group.

It was not until Singer (e.g., 1943b, 1949, 1962, 1967, 1973, 1975, 1977) became interested in the genus, however, that any attempt was made to organize and formulate a coherent classification for *Laccaria* based on the world mycota. To date, Singer's publications on the genus are the most comprehensive and influential. His classification has been the starting point for this study and for most other systematic research on the genus since the 1940s.

Several alternative classifications have been published, including those of Bon (1983), Clémençon (1984), and Ballero and Contu (1989). Additionally, numerous mycological surveys that included *Laccaria* have been published by various authors for most areas of the world. Some of these publications include Rea (1922), Kühner and Romagnesi (1953), Dennis et al. (1960), Orton (1960), Phillips (1981), Moser (1983), Dennis (1986), Ballero and Contu (1987), Watling (1987), and Mueller (1991a) for temperate Europe; Möller (1945), Lange (1955), Kobayasi et al. (1967), Miller et al. (1982), and Gulden and Jenssen (1988) for the Arctic; Vellinga (1986) for India; Malençon and Bertault (1975) for North Africa; Heinemann (1964, 1966) and Pegler (1977) for East Africa; Binyamini (1973, 1976) for Israel; Stevenson (1964) and McNabb (1972) for New Zealand; Imai (1938) and Hongo (1959, 1971) for Japan; Singer (1952, 1953), Singer and Digilio (1952), Singer and Moser (1965), and Horak (1979) for South America; and Singer (1957), Aguirre-Acosta and Pérez-Silva (1978), and Montoya-Bello et al. (1987) for Mexico.

North America North of Mexico

Schweinitz (1822, 1834) was the first American mycologist to publish on the North American mycota. In his list of all the then-known fungi from America, Schweinitz (1822) included *Agaricus* (*Omphalia*) *bellus* and *A.* (*Omphalia*) *farinaceus.* In 1834 he included *A.* (*Clitocybe*) *laccatus, A.* (*Clitocybe*) *amethystinus,* and *A.* (*Clitocybe*) *bellus.* Several collectors working in North America, including Curtis, Lea, Sullivant, and Wright, sent specimens and notes on American fungi to various workers in Europe, especially Berkeley, and several new species (e.g., *A. ohiensis* Montagne and *A. ochropurpureus* Berkeley) were discovered and published in this manner.

Ellis (1874) described *A.* (*Clitocybe*) *trullissatus* from the sand dunes of New Jersey, and thus became the first North American to designate a new species in this group. Charles H. Peck was the first North American worker who studied and published on the group in some detail (Peck, 1890, 1893, 1895, 1897, 1903, 1907, 1912). *Laccaria amethystina* Cooke, *L. laccata, L. ochropurpurea*

(Berk.) Peck, *L. striatula* (Peck) Peck, and *L. tortilis* (Bolt.) Cooke were included in the *North American Flora* (Murrill, 1914). These same taxa were included in a study of *Laccaria* in North Carolina (Coker and Beardslee, 1922).

Little systematic work was done on the genus again until Singer described *L. tetraspora* from Florida and *L. calospora* and *L. laccata* var. *carbonicola* from Massachusetts (Singer, 1946, 1967, 1973, respectively). Mueller and Sundberg (1981) presented a treatment for the genus from southern Illinois. Lahaie undertook a study of the genus from eastern Canada for his master's thesis (1981), but his results have not been published. Mueller (1984, 1991b) described six new species from the continental United States and Canada.

Materials and Methods

Morphological Analyses of Basidiomata

Extensive collecting was undertaken throughout the United States and parts of eastern and western Canada. The following states and provinces were sampled: British Columbia, California, Colorado, Florida, Georgia, Idaho, Illinois, Kentucky, Louisiana, Massachusetts, Michigan, Minnesota, Mississippi, New York, North Carolina, Nova Scotia, Ohio, Ontario, Oregon, South Carolina, Tennessee, Texas, Virginia, West Virginia, Washington, Wisconsin, and Wyoming. Field work was also undertaken in Sweden, Mexico, Costa Rica, and much of South America as part of an ongoing project to produce a world monograph of the genus and to obtain comparative material. Dried specimens on loan from numerous herbaria (see Acknowledgments), including most extant type specimens, were also examined.

Collections were made and assembled using standard techniques (Smith, 1949; Largent, 1977). Descriptive terms were taken from Snell and Dick (1971) and Largent (1977). Unless otherwise noted, color names within parentheses and quotation marks are from Ridgway (1912), colors from Kornerup and Wanscher (1978) are listed by (page-column-row), and color names outside of parentheses are author-generated. Color names followed by M&P were taken from Maerz and Paul (1930).

Basidiomata were preserved by warm-air drying and deposited in either F, TENN, UPS, or WTU (Holmgren et al., 1981). Most examinations were made directly using either a Nikon Model S-Kt research microscope, a Zeiss Universal photomicroscope, or a Zeiss RA standard microscope equipped with both bright field and phase contrast optics. Recent data acquisition and remeasurements were made using JAVA 1.31 (Jandel Video Analysis Software, 1989) running on an AT&T 6386 computer from images captured through an Olympus BH-2 microscope with Nomarski differential interference optics. Illustrations of micromorphological characters were made with the aid of a drawing tube. All measurements were made on material mounted in 3% KOH. Iodine reactions were determined in Melzer's reagent and the cyanophilic reaction was determined in cotton blue (Kotlaba & Pouzar, 1964; Singer, 1972; Largent et al., 1977). Descriptive terminology is from Snell and Dick (1971) and Largent et al. (1977).

Micromorphological data used in taxon descriptions were based on a complete, detailed examination of at least five (when possible) representative collections per taxon. The number of collections examined was dependent upon the availability of material and the amount of variability encountered within the taxon. All specimens listed in Specimens Examined (Appendix A) were examined, and any deviations from the norm were noted.

Measurements and observations were taken from several basidiomata per collection to check for uniformity. At least 10 randomly sampled cheilocystidia, pleurocystidia, and terminal cells of cuticular hyphae, and 15 randomly sampled basidia were measured per collection. Width and diameter measurements of these elements were taken at the widest point and rounded to the nearest 0.5 μm. Arrangement of hyphae comprising the pileipellis was observed in both radial and scalp sections.

All basidiospore measurements were taken from hymenial tissue and not from spore prints, in order to treat all specimens equally. The number of basidiospores measured and the number of collections examined for calculating mean size ($= \bar{x}$) and length/width ratio ($= Q$) are included in brackets with basidiospore size data to give some indication of reliability of these data (Bas, 1974). When available, data on basidiospores from additional collections were included in basidiospore size range data. Ranges of collection means ($\bar{x}$, $\bar{Q}$) for basidiospore data, rather than overall mean values for the taxon, are provided to give a better indication of intraspecific variation. Basidiospore size data are always given without ornamentation and hilar appendix, with the hilar appendix in profile. Means and other descriptive statistics were obtained us-

ing SAS for Personal Computers, Version 6.03 (SAS, 1985).

Scanning Electron Microscope Analyses

Lamellar fragments from air-dried collections were rehydrated in an acetone series, fixed in 2.5% glutaraldehyde in phosphate buffer for 3–4 hr at 4° C, dehydrated in an acetone series, and critical point dried in a Balzers CPD 030 apparatus with CO_2 as the transition fluid (Cheeseman & Grund, 1985). Samples were then attached to aluminum mounts with double-stick tape and coated with gold in a Denton Vacuum Desk II sputter coater. Basidiospores were examined and micrographs were taken at 20 kV with an Amray 1810 scanning electron microscope.

Somatic Culture Mat Analyses

The following procedure was employed to obtain heterokaryotic tissue cultures of *Laccaria*. Small pieces of tramal tissue excised from the pileus–stipe interface were aseptically placed on modified Melin Norkrans medium (= MMN) plus benomyl (10 mg/L) in disposable test tubes (Marx, 1969; Molina & Palmer, 1982; Mueller, 1984). The benomyl was added to reduce ascomycetous contamination. Six to 10 replicates were taken for each collection utilized. Subculturing of each resulting isolate was undertaken until a pure culture was obtained. Stock isolates were then transferred to tubes containing modified MMN or N6:5 medium (Fries, 1983a) and stored in the dark at 2–4° C. Voucher herbarium material of all specimens used for tissue cultures was described and deposited in F, TENN, UPS, and WTU. All isolates are housed in the mycological culture collection at the Field Museum of Natural History.

Culture mat analyses were based on the classic work of Nobles (1948, 1965). Five-millimeter round plugs of agar containing hyphal tips taken from the advancing zone of each of 2-wk-old "stock" plates were transferred to the edge (mycelium side down) of a Petri plate containing 15–20 ml of either MMN, malt extract agar (= MEA), or potato dextrose agar (= PDA). Seven replicates of each medium for each isolate were inoculated and placed in a dark incubator at 24° C. Macromorphological descriptions were made during the third and sixth weeks. Photographs of representative isolates were taken during the fourth week, and micromorphological characters were examined during the sixth week.

Macromorphological characters noted included (1) radius of the culture mat, (2) form and character of the advancing zone, (3) mat color and topography, and (4) the presence or absence of exudates. Terminology used was taken from Nobles (1948, 1958b, 1965).

Micromorphological characters were observed by mounting hyphae from the advancing zone, mat, and plug of each isolate in 3% KOH and examining the slide under phase contrast. Micromorphological characters examined included the presence or absence of (1) modified hyphae, (2) chlamydospores or oidia, etc., and (3) basidiomata or hymenial structures such as basidia or cystidia along the mat surface. Descriptive terminology used was that of Nobles (1948, 1965).

Extracellular oxidase activity of each isolate was tested using both the Bavendamm (Davidson et al., 1938, 1942) and gum guaiac (Nobles, 1958a, 1965) tests (Mueller, 1984).

Intra- and Intercollection Pairing Analyses

Homokaryotic isolates were obtained following the techniques of Fries (1983a,b) and Fries and Mueller (1984). Homokaryotic isolates originating from one basidioma were assigned a stock number. Within a stock, each isolate received a unique extension number. All isolates are stored at 2–4° C on N6:5 medium in the mycological culture collection at the Field Museum of Natural History.

Intra- and interstock pairing analyses were carried out following the procedures outlined in Mueller and Gardes (1991). Isolates to be tested were placed ≤ 10 mm apart on N6:5 plates and allowed to grow together (2–4 wk). After an additional 1 wk or more, plugs of tissue were cut from the interface and placed on fresh N6:5 plates. Mycelia growing from these plates were checked for the presence or absence of clamp connections by examining them through the bottom of the inverted Petri plate at 200× magnification. Pairings resulting in hyphae that bore clamp connections were considered positive; those that did not yield clamped hyphae were scored as negative. Two or more testers for each stock, each containing different mating type alleles, were used when possible. As in Mueller and Gardes (1991) and Mueller (1991c), the terms noncompatible and intracompatible are restricted to intrastock pairings. I used the terms intersterile for intercollection pairings

that did not form clamp connections and intercompatible (rather than interfertile) for positive intercollection matings because data regarding fruiting and progeny analysis were not available.

Discussion of Systematic Characters

Many *Laccaria* taxa appear similar on superficial examination. Closer examination of the macro- and micromorphological variation, when correlated with cultural and molecular data, allows for the segregation of taxa in this phenotypically variable group. The following discussion on the delimiting characters within *Laccaria* is restricted to the 20 North American taxa, of which 18 were collected, photographed, and described during the course of this study.

Basidioma Macromorphology

COLOR—Basidioma and lamellar colors are the most diagnostic macromorphological characters. A major problem with this suite of characters is that the pigments responsible for these colors are unknown in many groups of agarics, including *Laccaria* (e.g., W. Steglich, Univ. Bonn, Germany, pers. comm., informed me that the pigments in *L. amethystina* oxidize very readily upon extraction and would take special care to analyze). Currently, it is not possible to determine homology between the pigment(s) in either the orange-brown or violet-colored *Laccaria* or to determine the primitive condition via comparison with presumably related genera (outgroup comparison). As mentioned in the section on Phylogenetic Considerations, I have made the assumption that the pigment(s) are homologous within these two groups of *Laccaria* (orange-brown vs. violet). Assumptions of homology between the pigments in *Laccaria* and pigments in potential outgroup taxa could not be made.

Because all members of the genus are hygrophanous, especially those taxa with violaceous to purple basidiomata, it is important to note the color of the pileus both when fresh and in successive stages of fading. This is most important in *L. amethysteo-occidentalis* G. M. Mueller, *L. amethystina,* and *L. vinaceobrunnea* G. M. Mueller. Basidiomata of all three are bright violet to purple when young and fresh but differ markedly in their color changes associated with age (see descriptions). *Laccaria ochropurpurea* and *L. trullissata* (Ellis) Peck are light violaceous when very young but soon become buff or red-brown at maturity.

Basidiomata of specimens of most other *Laccaria* are some shade of orange-brown to flesh color. Because of the large amount of color variation found within these taxa (from light buff to a strong orange-brown or red-brown), basidioma color can rarely be used to delimit taxa in this large group.

North American species of *Laccaria* exhibit either pinkish flesh color to buff color or violaceous to purple lamellae. All of the taxa with violaceous to purple basidiomata plus *L. ochropurpurea* and *L. trullissata* have bright violet to dark purple lamellae. Basidiomata of *L. bicolor* (Maire) Orton, *L. nobilis* G. M. Mueller, and, possibly, *L. maritima* (Teodorowicz) Singer *ex* Huhtinen have light pinkish violet to wine-colored lamellae that occasionally fade to a pinkish color with age. All other North American taxa have flesh-colored lamellae. In some instances the lamellae of large, older specimens may develop a vinaceous appearance, but an examination of younger specimens should alleviate any confusion that this may cause. Basidiomata of *L. fraterna* (Cooke & Massee: Saccardo) Pegler, which probably is an introduced taxon, have rosy-pink lamellae when fresh.

The color of the mycelium at the base of the stipe (= basal mycelium) is also systematically important in *Laccaria.* The basal mycelium can be either violet or white. In addition to *L. trichodermophora* G. M. Mueller and *L. oblongospora* G. M. Mueller, all of the taxa with violet lamellae consistently have a violet basal mycelium. In all of these taxa, however, the basal mycelium occasionally fades to white with age.

BASIDIOMA SIZE—Although often highly variable due to differences in age and environmental conditions, the size of the basidioma can be diagnostic in some instances. Most taxa have mature basidiomata of moderate size (pileus 20–50 mm broad, stipe up to 60 mm long), so those taxa that consistently have larger or smaller basidiomata are noteworthy. *Laccaria montana* Singer, *L. ohiensis, L. pumila* Fayod, and *L. tortilis* are characterized by being small (pileus rarely up to 30 mm broad); *L. amethysteo-occidentalis, L. nobilis, L. ochropurpurea,* and *L. trullissata* often have pilei greater than 60 mm broad.

The stature of the basidioma can also be systematically important. *Laccaria maritima, L. ochropurpurea,* and *L. trullissata* are usually robust (stipe diameter > 7 mm at apex), while all of the taxa characterized by having small basidiomata,

plus *L. striatula* (Peck) Peck, are generally gracile (stipe diameter ≤ 4 mm at apex).

Stipe and pileus ornamentation characteristics are often associated with size. Although most of the small taxa appear glabrous to finely fibrillose when fresh, taxa with large basidiomata, such as *L. nobilis,* often have pilei that become scaly to squamulose due to cuticular diffraction. Additionally, large basidiomata frequently have stipes clothed with pronounced longitudinal striations that can form reticulations or become scaly near the stipe apex (e.g., *L. amethysteo-occidentalis, L. nobilis, L. ochropurpurea,* and *L. trullissata*).

Basidiospore Color in Mass—Except for *L. amethystina* and *L. ochropurpurea,* which can have either white or light violet basidiospore deposits, all North American taxa have white spore prints. The color of the print will occasionally yellow with age.

Additional Macromorphological Characters—Characters such as type and degree of pileus striations, pileus shape, lamellar attachment and thickness, pileus and stipe context, or odor and taste are not systematically significant within *Laccaria.* Except for color and, in some instances, size, micromorphological and cultural characters must be used to differentiate taxa.

Basidioma Micromorphology

Basidia—The number of basidiospores borne per basidium is significant in *Laccaria.* Although many other genera of agarics have species with varying number of sterigmata in one basidioma (e.g., Hesler & Smith, 1963; Singer, 1986), the character appears to be consistent in *Laccaria.* In all of the material examined, the vast majority of the basidia observed in a mount had the same number of sterigmata. Basidia examined from material of *L. fraterna, L. pumila,* and *L. tortilis* bore 2(–3) basidiospores. All of the rest of the North American taxa had 4-sterigmate basidia. Bisterigmate basidia generally had longer and stouter sterigmata. No other basidial characters appeared to have systematic significance.

Basidiospores—Basidiospore shape is of critical importance in designating species. Basidiospore shape terms used in this study are based on Bas (1969), with basidiospore shape described in terms of length–width ratios (Q): globose = 1.0–1.05, subglobose = 1.06–1.15, broadly ellipsoid = 1.16–1.23, ellipsoid or amygdaliform = 1.24–1.6, oblong = 1.65–2.0, cylindrical or subfusiform > 2.0.

Specimens of most North American taxa have basidiospores that are subglobose to broadly ellipsoid. *Laccaria proxima* (Boudier) Patouillard and *L. oblongospora* are characterized by having ellipsoid to oblong basidiospores; basidiospores in specimens of *L. trullissata* and *L. maritima* are oblong to subfusiform. Globose basidiospores are found in specimens of *L. amethystina, L. ochropurpurea, L. ohiensis, L. striatula,* and *L. tortilis.*

Basidiospore size is also an important systematic character in some instances. Individuals of most taxa have overall mean basidiospore lengths of 8–9 μm. However, *Laccaria bicolor, L. longipes* G. M. Mueller, *L. nobilis,* and *L. trichodermophora* are characterized by having relatively small basidiospores ($\bar{x}$ < 8 μm long), and specimens of *L. fraterna, L. montana, L. pumila,* and *L. tortilis* have larger basidiospores ($\bar{x}$ = 9.5–13 μm long). The basidiospores of *L. maritima* and *L. trullissata* are greater than 13 μm in length.

Except for *L. trullissata,* which has finely roughened basidiospores (figs. 41a, 57b–d, 72d), all species of *Laccaria* have echinulate basidiospores with a plage near the hilar appendix. Echinulae length and width at attachment are important systematic characters within the genus.

Electron microscopic examinations of basidiospores using the carbon surface replica technique (Bigelow & Rowley, 1968; Pegler & Young, 1971), transmission electron microscopy (= TEM) (Besson & Kühner, 1971), and scanning electron microscopy (= SEM) (Pegler & Young, 1971; Mueller & Sundberg, 1981; Irving et al., 1985; Mueller, 1991c; this paper, figs. 53–58) have shown details of the surface and ornamentation characteristics. At my request, A. von Hofsten (Institute of Physiological Botany, University of Uppsala, Uppsala, Sweden) examined basidiospores from collections of several *Laccaria* species (*L. bicolor, L. maritima,* and *L. proxima*) and from a collection of *Hydnangium carneum* Wallroth *apud* Klotzsch under the TEM (von Hofsten, unpubl.). The results of this study were concordant with the findings of Besson and Kühner (1971). The basidiospore echinulae of all *Laccaria* species examined to date, plus the gasteroid relative *Hydnangium carneum,* are composed of microtubules that run perpendicular to the epispore (Besson & Kühner, 1971; Kühner, 1980). This type of echinulae ultrastructure appears to be unique to *Laccaria, Hydnangium,* and probably *Podohydnangium* Beaton, Pegler & Young (not examined under TEM). Echinulae ultrastructure is the primary synapomorphy that supports the recognition of these

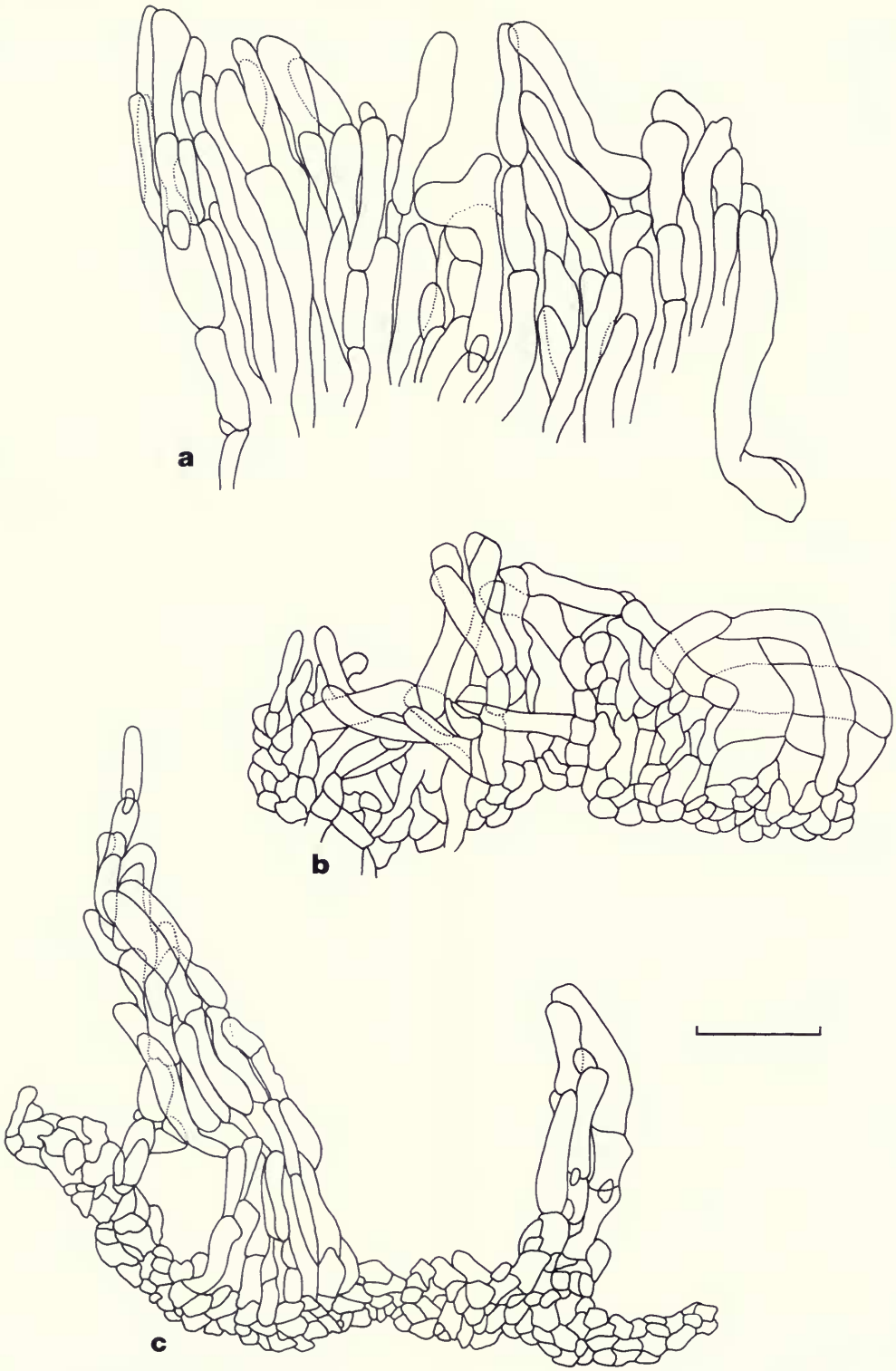


FIG. 1. Representative pileipellis arrangements occurring in North American taxa of *Laccaria*: **a,** trichodermium; **b,** interwoven; **c,** interwoven with scattered ± perpendicular fascicles of hyphae. Scale line = 10 μm.

three genera as a monophyletic group (see Phylogenetic Considerations).

The basidiospores in all taxa are nonamyloid and acyanophilic.

PILEIPELLIS—Three types of hyphal arrangements were found in *Laccaria* (fig. 1a–c): a trichodermium, observed in most collections of *L. trichodermophora*; interwoven as in collections of *L. ochropurpurea*; or interwoven with scattered nearly perpendicular fascicles of hyphae (the most common pileipellis encountered). In *L. vinaceobrunnea* and in some collections of *L. amethystina,* the hyphae of the pileipellis are interwoven with very numerous, long, individual hyphae that are arranged nearly perpendicular to the pileus surface. If the erect hyphae were aggregated closer together, the pileipellis could be described as a palisadoderm.

Pileipellis hyphae were often encrusted with a light to moderate yellowish brown pigment. In young specimens of *L. amethystina, L. amethysteo-occidentalis,* and *L. vinaceobrunnea,* the hyphae occasionally appeared vinaceous brown in mass.

Although data on the size of the terminal cells[1] are presented in the species descriptions, the size and shape of these cells appeared to have little systematic significance. Additionally, the underlying tramal layer was morphologically undifferentiated and systematically uninformative.

CHEILOCYSTIDIA—The cheilocystidia of most *Laccaria* species, if present, are little more than elongate, filamentous hyphae that extend beyond the basidia and basidioles. Only in specimens of *L. amethystina, L. amethysteo-occidentalis,* and *L. vinaceobrunnea* were large (overall mean dimensions up to 58 × 10 μm), clavate to strangulate, abundant cheilocystidia observed. In many collections these cheilocystidia formed a nearly sterile layer. The uniqueness and consistent presence of large cheilocystidia in these three *Laccaria* taxa was a good diagnostic character for herbarium material that lacked macromorphological notes.

Pleurocystidia were not seen in any North American material of the genus. Morphologically undifferentiated caulocystidia are present in some taxa.

[1] Because there is a nuclear continuity between hyphal segments through the septum, each of these segments should be termed a hyphal element and not a cell. For the sake of avoiding confusion, however, the term cell is used throughout this paper.

ADDITIONAL MICROMORPHOLOGICAL CHARACTERS—The constant occurrence of clamp connections at virtually every septum and a parallel or rarely subparallel lamellar trama are important generic characteristics of *Laccaria.* Additionally, all hyphae were nonamyloid and, unless otherwise specified, hyaline in KOH.

The hyphae comprising the basal mycelium were tightly interwoven and either morphologically undifferentiated or barrel-shaped. The diameter of these hyphae appeared to vary as much within a taxon as between taxa.

Basidiospore and Basidium Cytology

Kühner (1980, 1984) emphasized the occurrence of multinucleate basidiospores in *Laccaria* in his decision to treat *Laccaria* in a family separate from other genera traditionally placed in the Tricholomataceae. These reports prompted us to investigate further the nuclear behavior in species of *Laccaria* and *Hydnangium.* To determine the significance of basidiospore and basidium cytology in the systematics of *Laccaria,* cytological studies on several species of *Laccaria* were carried out in J. F. Ammirati's laboratory (Department of Botany, University of Washington, Seattle).

Several questions were addressed during the course of this study, including: (1) Is the occurrence of multinucleate basidiospores a characteristic of the genus, or is this feature restricted to a few taxa? (2) Where does postmeiotic mitosis occur in taxa with multinucleate basidiospores?

Basidia and basidiospores of representative specimens of each of the 11 *Laccaria* species and *Hydnangium carneum* listed in Table 1 were examined using fluorescent microscopy. Glutaraldehyde-fixed and nonfixed tissues were mounted in Hoechst fluorescent dye and examined using a Zeiss fluorescence microscope with 365 nm excitation and 480 nm emission filters.

Multinucleate basidiospores appear to be a constant feature within *Laccaria,* as they occur throughout the genus from the putatively primitive *L. proxima* to diverged taxa such as *L. tortilis, L. amethysteo-occidentalis,* and *L. trullissata* (table 1). These data also are concordant with the hypothesis of the close relationship of *Laccaria* to *Hydnangium.* According to Kühner (1980, 1984), the occurrence of multinucleate basidiospores is rare in the Tricholomatales *sensu* Kühner (±Tricholomataceae *sensu* Singer).

TABLE 1. Number of nuclei observed in the basidiospores of examined *Laccaria* and *Hydnangium* visualized with Hoechst fluorescent dye.

Taxon	No. Basidiospores per Basidium	No. Nuclei per Basidiospore
L. amethysteo-occidentalis	4	2
L. bicolor	4	2
L. fraterna	2	4
L. laccata var. *pallidifolia*	4	2
L. montana	4	2
L. ochropurpurea	4	2
L. proxima	4	2
L. pumila	2	4
L. tortilis	2	4
L. trullissata	4	2
L. vinaceobrunnea	4	2
H. carneum	2	4

The following is a summary of results obtained during studies of tetra- and bisterigmate *Laccaria* taxa (*L. bicolor, L. galerinoides* Singer, *L. laccata* var. *pallidifolia, L. montana, L. proxima, L. proximella* Singer, *L. pumila, L. tortilis,* and *L. vinaceobrunnea*) using Giemsa-stained material examined under bright field microscopy. Detailed results will appear in a separate publication (G. J. Mueller, G. M. Mueller, L. Shih & J. F. Ammirati, in prep.). The dikaryotic basidium of both tetra- and bisterigmate *Laccaria* is more or less cylindrical in shape. The two nuclei move to the center of the basidium and fuse to form the diploid nucleus, during which time the basidium gradually enlarges and becomes clavate in shape. The diploid nucleus then moves to the apical region of the basidium, where meioses I and II occur. These divisions are chiastic, and the resulting four nuclei migrate to the center of the basidium. During these events the basidium enlarges to its mature size and shape, and sterigmata with developing basidiospores are formed. In most cases, once the basidiospores are fairly well developed, the nuclei begin to move through the sterigmata and into the basidiospores so that basidiospores from tetrasterigmate basidia each receive one nucleus, while those with bisterigmate basidia each receive two nuclei. In these cases the (nucleus) nuclei in the basidiospores then undergo a mitotic division so that basidiospores from tetrasterigmate basidia are binucleate and those of bisterigmate basidia are tetranucleate. Occasionally this postmeiotic mitosis occurs in the basidium before nuclear migration. In these cases, all eight nuclei migrate into the basidiospores. In both scenarios, mature basidiospores are multinucleate.

Tommerup and colleagues reported similar nuclear behavior for *L. fraterna* (Tommerup et al., 1991). According to them, however, nuclear behavior in *Hydnangium carneum* differs in that postmeiotic mitosis occurs in the basidium prior to migration into the basidiospores. Additional information on nuclear behavior in *Hydnangium* and *Podohydnangium* is necessary before it will be possible to determine if multinucleate basidiospores in *Laccaria* and these two genera are homologous. The *Hydnangium* used by Tommerup et al. (1991) is reported to have tetrasterigmate basidia, and the illustrated basidiospores are broadly ellipsoid and finely ornamented. This is in contrast to my concept of *H. carneum.* All of the collections that I have examined which are referable to this taxon have bisterigmate basidia that bear strongly echinulate, globose basidiospores. Similarly, published illustrations of basidiospores and basidia for this taxon usually depict globose, strongly echinulate basidiospores and bisterigmate basidia (e.g., Pegler & Young, 1979; Beaton et al., 1984; Castellano et al., 1989). Until a survey of other taxa in the genus is undertaken, and until phylogenetic relationships within the genus are resolved, it is not possible to determine the plesiomorphic condition for nuclear behavior in *Hydnangium.*

Somatic Culture Mat Morphology

Somatic culture mat studies based on the classic work of Nobles (1948, 1958b, 1965) were undertaken to obtain additional informative characters. Although becoming almost routine in studies of the wood-rotting Aphyllophorales and many groups of saprobic Agaricales, utilization of somatic culture mat data has only infrequently been used in systematic studies of fungi that form ectomycorrhizae. At least two factors are responsible for this. First, many of these fungi are recalcitrant to domestication (but see Hutchinson, 1990a,b; Hutchinson & Summerbell, 1990). Second, early work indicated that cultures of fungi that form ectomycorrhizae exhibited few morphological differences (e.g., Zak & Bryan, 1963; Zak & Marx, 1964).

Fries and Mueller (1984) reported no differences in morphology (except for the presence or absence of clamp connections) between homokaryotic and heterokaryotic isolates. Occasional differences in

growth rate, color intensity, and other features have since been detected between heterokaryotic isolates obtained via tissue culture, isolates originating as polysporous cultures, and homokaryotic isolates (Kropp et al., 1986; Kropp & Fortin, 1988; Mueller, unpubl.). While overall similarities are normally observed, care must be used when employing isolates of different origin for comparative studies. The following data are based primarily on isolates of tissue culture origin.

MACROMORPHOLOGY—The two primary diagnostic characters were the color of the culture mat on MMN and PDA (all isolates were white on MEA) and the rate of growth (expressed as the radius of the culture mat at week 3 and week 6) on each of the three media employed. Photographs of representative isolates are included as part of the description for a number of North American taxa (figs. 7, 10, 13, 31, 34, 37, 44).

Taxa that had white to off-white culture mats on all three media were *L. fraterna, L. laccata, L. longipes, L. montana, L. ohiensis, L. proxima, L. pumila,* and *L. striatula.* No isolates were obtained of *L. maritima* or *L. tortilis.* Isolates of all other North American taxa were violet to purple on PDA and MMN. To date there is a 100% correlation between basal mycelium color and somatic culture mat color. This supports the utility of basal mycelium color as a good delimiting field character.

Although a slight bleaching of color was often noted on the reverse side of the culture mat, no significant color changes occurred. Additionally, no exudates were apparent.

Along with color, the rate of growth could be used to delimit taxa. Isolates of most taxa grew at a moderate rate on all three media (20–50 mm on PDA, 30–70 mm on MMN, and 40–70 mm on MEA—all at week 6). Isolates of *L. amethysteo-occidentalis, L. montana,* and *L. ohiensis* grew much more slowly (often only 10–15 mm after 6 weeks' growth). Conversely, isolates of *L. bicolor, L. nobilis, L. oblongospora,* and *L. trichodermophora* grew more rapidly.

Terminology used in discussing mat and margin texture was from Nobles (1948, 1965).

Except for an occasional pruinose, aerial layer of hyphae observed in older cultures of many taxa, the mycelium of all of the isolates grew tightly appressed to the agar surface. The transparency of the culture mat was an outcome of the thickness and intricacy of the interwoven mat. All isolates exhibited a felty, thick culture mat on PDA. The mat texture on both MMN and MEA varied from silky to subfelty to felty. Often the mat was thickest near the inoculation plug. In most cases, culture mats were of uniform thickness from the plug to the margin. In some taxa, however, variously distributed thicker zones were observed. These thicker zones could be scattered, small sectors (e.g., some *L. trichodermophora* isolates on MMN and *L. bicolor* on MEA), two or three concentrically arranged bands (e.g., *L. amethysteo-occidentalis* on MEA), or radially arranged pie-shaped or dendritic sectors radiating away from the inoculation plug (e.g., *L. trichodermophora* on PDA).

When describing the margin texture and color, I refer to the advancing zone of the culture mat. This zone is generally somewhat thinner than the rest of the mat and can be either a discrete, easily recognizable area or not well differentiated. On all three media, this zone was always silky to subfelty and thus presented little systematically informative data.

All of the isolates had the same musty odor on all three media.

Growth or diffusion zones were not obtained on gallic acid agar with any of the isolates. Immediate reaction to the gum guaiac drop test was observed only in some isolates of *L. bicolor.* I did not attempt other tests for the presence or absence of extracellular enzymes because of these basically negative results. Hutchison (1990a), however, performed drop tests of 1-naphthol and p-cresol on numerous isolates of ectomycorrhizal fungi growing on several different media and reported the presence of tyrosinase activity in all of the *Laccaria* that he tested (i.e., *L. bicolor, L. laccata, L. ochropurpurea,* and *L. proxima*). Only *L. bicolor* showed any indication of laccase activity (Hutchison, 1990a).

Hutchison (1990b) investigated enzymatic degradation of various carbon and nitrogen compounds by fungi that form ectomycorrhizae. Using the same taxa listed in the previous paragraph, he reported that *Laccaria* did not degrade pectin, lipid, amylose, or gelatin but showed various levels of degradation of casamino acids and urea. Hutchison and Summerbell (1990) reported that these same isolates gave red to violet reactions to Diazonium Blue B when treated with cold KOH and yellow reactions without cold KOH treatment.

MICROMORPHOLOGY—There was little hyphal differentiation observed within and between the *Laccaria* isolates examined during this study. No spores were formed in culture.

In all isolates, the vast majority of hyphae were morphologically undifferentiated, with clamp connections at nearly all septa (fig. 2a). Scattered among

these sparsely branched hyphae were subcoralloid to coralloid hyphae (fig. 2b,c) and/or irregularly swollen hyphae (fig. 2d). All hyphae were hyaline in KOH, except where noted. Localized, slightly thick-walled swellings were often observed in plates of all taxa (fig. 2e). These swellings could either be terminal or intercalary and could be found in chains of two to four. They are likely a response to water stress, as they become more abundant when the agar in Petri plates loses moisture. Hutchison (1989) reported similar swellings from numerous isolates of ectomycorrhizal fungi.

Pantidou et al. (1983) reported the presence of holoblastic conidia from a purported culture of *Laccaria laccata.* Hutchison (1989), however, reported that these structures were secretory cells of a *Pleurotus* sp. and that the isolate used by Pantidou et al. (1983) was from a species of that genus, not *L. laccata.*

Intra- and Intercollection Pairing Reactions

Information on intra- and intercollection pairing reactions has only recently been employed for systematic and biological studies of fungi that form ectomycorrhizae (Fries, 1987). Fries (1977) first reported the successful germination of basidiospores from collections of *Laccaria.* Several years later he reported the occurrence of several intersterility groups within *L. laccata sensu lato* (Fries, 1983a). Fries and Mueller (1984) later determined that these intersterility groups were referable to separate species. They documented a good correlation between the identified intersterility groups and species based on morphological characters, using Swedish isolates of *L. amethystina, L. bicolor, L. laccata,* and *L. proxima.* Intraspecific pairings of these Swedish isolates revealed a high incidence of intercompatibility in three of these species (all but *L. laccata*). Two intersterility groups were detected within Swedish isolates from morphologically similar collections identified as *L. laccata.* The two intersterility groups within *L. laccata* were treated as sibling species because they could not be delimited on morphological characters (Fries & Mueller, 1984; Mueller & Vellinga, 1986). Studies by Kropp and Fortin (1988) and Doudrick and Anderson (1989) documented the occurrence of two or more intersterility groups within the North American population of *L. bicolor.*

When used in conjunction with data from other analyses, information on intercollection pairing reactions has proven useful for circumscribing taxa (Mueller & Gardes, 1991; Mueller, 1991c). Mueller and Gardes (1991) reported three intersterility groups within the examined material of North American *L. bicolor.* Intragroup intercompatibility was high, and most intergroup pairings were intersterile. These groups could be circumscribed on both morphological and molecular characters and consisted of isolates of *L. bicolor sensu stricto, L. nobilis,* and *L. trichodermophora.* Questions remain as to the relationship of Swedish material, morphologically similar to North American material of *L. bicolor sensu stricto,* to the three North American taxa. The two isolates of Swedish origin used as testers were 100, 57, and 21% intercompatible with North American isolates of *L. bicolor, L. nobilis,* and *L. trichodermophora,* respectively.

Interstock pairing reactions were also useful in a study of the *L. laccata* complex (Mueller, 1991c). However, because isolates of *L. laccata* var. *laccata* were not available for inclusion in these analyses, some of the systematic conclusions remain tentative. Several North American intersterility groups were detected, and all tested North American isolates were intersterile with both of the intersterility groups reported from Sweden by Fries and Mueller (1984). Most, but not all, of these groups could be delimited morphologically. Molecular divergence (detected through analyses of restriction fragment length polymorphisms of mitochondrial and nuclear ribosomal DNA) was also detected between several of these intersterility groups (Gardes et al., 1990, 1991a; see below). Intersterility groups that could be delimited from morphological characters were recognized at the species level (i.e., *L. laccata, L. longipes, L. montana, L. ohiensis,* and *L. striatula*).

As in the study on the *L. bicolor* complex (Mueller & Gardes, 1991), data obtained to date do not resolve questions concerning potential gene exchange between geographically distant populations of some putatively cosmopolitan species in the *L. laccata* complex (Mueller, 1991c). The most commonly collected North American taxon in the complex is *L. laccata* var. *pallidifolia.* Mueller and Vellinga (1986) and Mueller (1991a) reported this taxon as being abundant in Europe. However, North American and Swedish isolates referable to this taxon are intersterile (Mueller, 1991c). Unfortunately, representative Swedish material of this taxon was not included in the studies of Gardes et al. (1990, 1991a,b), so data are not available on molecular divergence between the two populations. It is not possible to delimit collections from

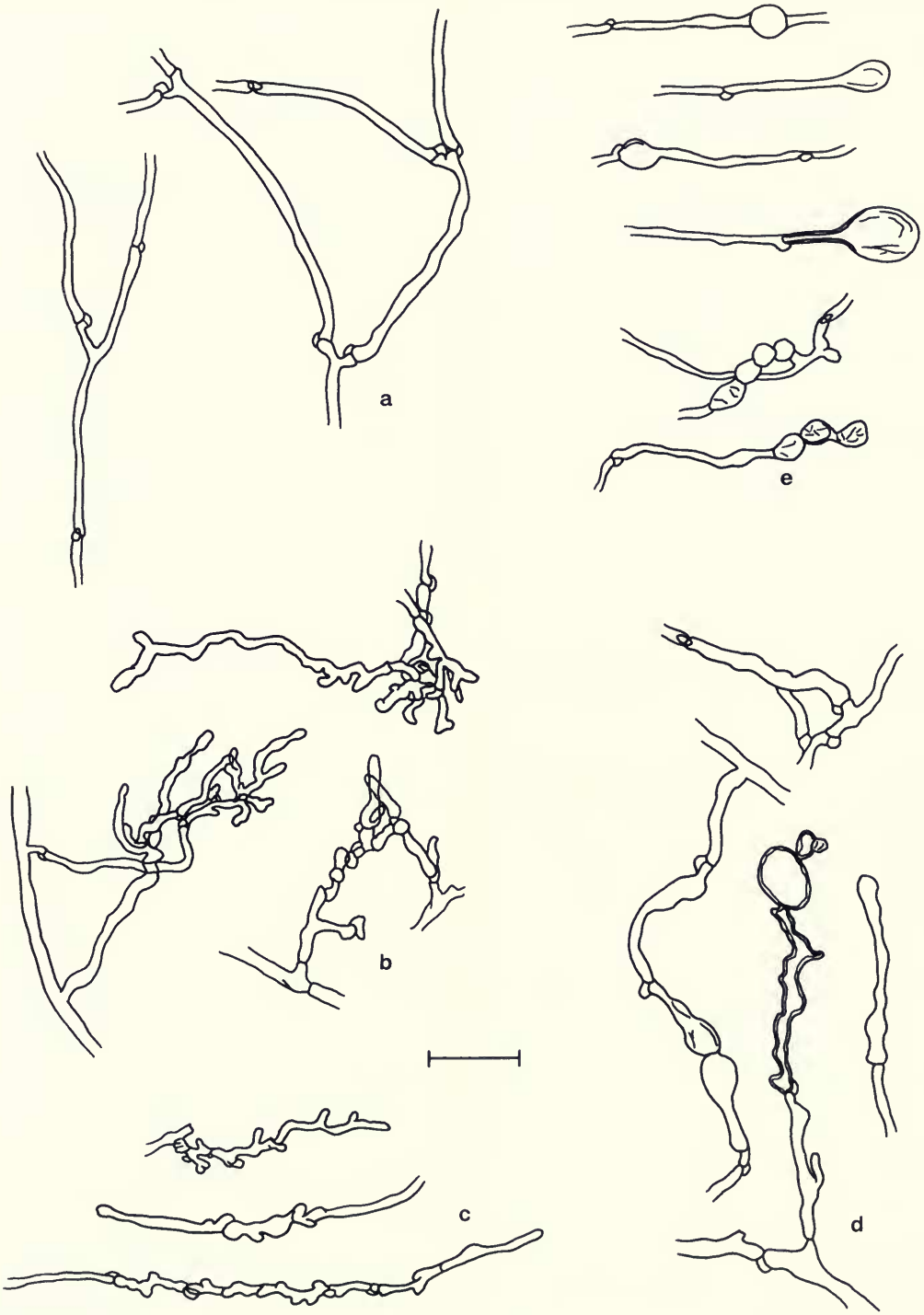


FIG. 2. Hyphal modifications observed during micromorphological analyses of 6-week-old somatic culture mats of *Laccaria* taxa: **a,** typical morphologically undifferentiated hyphae—note the presence of clamp connections and the regular branching pattern; **b,** coralloid hyphae—note the numerous, short, intertwining branches; **c,** subcoralloid hyphae; **d,** irregularly swollen hyphae; **e,** hyphae with terminal and intercalary swellings. Scale line = 10 μm.

the two populations based on morphology (Mueller, 1991c). For now, therefore, I treat these two potentially intersterile populations as contaxic.

Tested isolates of *L. amethysteo-occidentalis, L. amethystina, L. proxima,* and *L. vinaceobrunnea* were intersterile in all attempted interspecific pairings. Intraspecific pairings were nearly completely intercompatible within these species. However, homokaryotic isolates were available from only two or three stocks for most of these species, so it was not possible to rigorously test the degree of intraspecific intercompatibility.

In this study I have delimited species so that they are presumably monophyletic and are diagnosable by a unique combination of character states. Data from intercollection pairings were used to help identify groups to analyze in detail for potential morphological and molecular divergence. Because data on morphology, breeding, and ecology are not always concordant, it is inadvisable to rigorously adhere to the biological species paradigm (see discussions in Mishler & Donoghue, 1982; Donoghue, 1985; de Queiroz & Donoghue, 1988, 1990; Cracraft, 1990; Vilgalys, 1991).

Restriction Fragment Length Polymorphisms of rDNA and mtDNA

It is not yet possible to routinely obtain in vitro basidioma production for any species of *Laccaria,* or most other fungi that form ectomycorrhizae. One consequence of this inability to obtain the complete life cycle for these organisms is that it is impossible to carry out genetic analyses or to determine if intercompatible isolates are fertile (would produce viable progeny). This problem, coupled with the fact that the ability to mate is a plesiomorphic character state (e.g., Donoghue, 1985), makes it necessary to have data from other analyses to substantiate hypotheses of gene exchange between populations. Gardes et al. (1990, 1991a) obtained data on restriction fragment length polymorphisms (RFLPs) for both nuclear ribosomal DNA (rDNA) and mitochondrial DNA (mtDNA) to (1) investigate possible genetic divergence between species and populations of the same putative species, (2) determine concordance of data obtained through morphological analyses and pairing analyses, and (3) evaluate molecular markers for isolate typing. The resulting data could not be used for phylogenetic reconstructions because the numerous length mutations that were detected within the segments of DNA analyzed prevented making the necessary assumptions of homology.

Comparable results were obtained with both mtDNA and rDNA for *L. amethystina* and *L. laccata sensu lato* (Gardes et al., 1990, 1991a; Mueller, 1991c), in which divergence was detected between North American and Swedish isolates of these taxa. Divergence was also detected between the tested intersterility groups of the North American *L. laccata* complex.

Conflicting results were obtained with mtDNA and rDNA within the *L. bicolor* complex (Gardes et al., 1990, 1991a; Mueller & Gardes, 1991). Divergence in rDNA was detected between the North American and Swedish populations but was not observed between North American intersterility groups. Conversely, divergence was detected between each of the North American intersterility groups but was not detected between North American and Swedish populations based on mtDNA polymorphisms. Additional European material needs to be examined to attempt to resolve this discrepancy. Only two Swedish isolates of *L. bicolor sensu lato* were utilized by Gardes et al. (1990, 1991a), so it is not possible to compare the amount of heterogeneity of either mtDNA or rDNA within North American and European populations. A possible explanation for these conflicting results is that Swedish *L. bicolor* migrated from a large North American population that contained a pool of mtDNA variation (J. W. Taylor, University of California, Berkeley, pers. comm.). The Swedish population would, therefore, contain only a subset of the mtDNA variation. Following migration, the North American population underwent divergence of morphological and pairing alleles, resulting in *L. nobilis* and *L. trichodermophora.* Some of the mtDNA variation within the original North American pool has subsequently been lost, as evidenced by the data on RFLPs, which uncovered more intraspecific than interspecific similarity in mtDNA for the three North American taxa. This hypothesis cannot be tested until a robust phylogeny for the group is obtained.

In Vitro Ectomycorrhizal Synthesis Results

Isolates of *Laccaria* are frequently used in applied and basic studies on ectomycorrhizae (see Kropp & Langlois, 1990). In vitro mycorrhizal synthesis studies employing the growth pouch technique of Fortin et al. (1983) are ongoing as part of my studies on *Laccaria.* Experiments were

run in a Plexiglas mycorrhizal synthesis chamber, the design for which was modified from plans from Steven Miller (University of Wyoming, Laramie, pers. comm.). The primary goals of these studies have been to further characterize species of *Laccaria* as well as to document the ability of particular species of *Laccaria* to form ectomycorrhizae with select tree species in the laboratory.

To date we have synthesized ectomycorrhizae between several *Laccaria* species (*L. amethysteo-occidentalis, L. bicolor, L. laccata* var. *pallidifolia, L. proxima,* and *L. striatula*) and the following North American trees: *Picea sitchensis* (Bong.) Carr., *Pinus ponderosa* Laws., *P. resinosa* Ait., and *Pseudotsuga menziesii* (Mirb.) Franco. Ectomycorrhizae have also been synthesized between *L. trullissata* and *Pinus resinosa* and between several South American isolates of *L. ohiensis* and seedlings of the southern beech, *Nothofagus obliqua* (Mirbel) Oerst.

Although macromorphology of the ectomycorrhizae varies with the species of host tree (e.g., degree of branching), their micromorphology is similar. In all material examined to date, a well-defined, 15–60 μm thick, tightly interwoven mantle of clamped, morphologically undifferentiated hyphae was formed. No cystidia-like elements have been observed. All infected short roots had a well-developed Hartig net that extended through 70–100% of the cortex. These data coincide with published data on *Laccaria* ectomycorrhizae.

Ecology and Distribution

Many species of *Laccaria* show some degree of host specificity. *Laccaria proxima* and *L. laccata* var. *pallidifolia* are the only North American taxa that appear to be associated commonly with both Fagaceae and Pinaceae. *Laccaria amethystina* and *L. ochropurpurea* appear to be associated solely with temperate hardwoods, especially species of *Quercus* and *Fagus grandifolia,* while *L. vinaceo-brunnea* has only been found under live oak, *Quercus virginiana. Laccaria ohiensis* has not been commonly collected in north temperate forests. In tropical and south temperate habitats, it is found associated with *Quercus* and *Nothofagus,* respectively.

All of the members of the *L. bicolor* complex (*L. bicolor, L. nobilis,* and *L. trichodermophora*) appear to be associated with Pinaceae in North America. *Laccaria trichodermophora* can shift hosts when members of the Pinaceae are not available—it has been found under tropical *Quercus* in Costa Rica (Mueller & Strack, unpubl.). Similarly, although *L. amethysteo-occidentalis* is most commonly found with conifers, especially *Pseudotsuga,* it can be found under *Quercus* in California.

Laccaria montana and *L. pumila* are commonly collected in arctic and alpine habitats, where they appear to be associated with Pinaceae (especially *Pinus*), *Salix,* and *Betula.*

Although many species of *Laccaria* can be encountered growing among mosses, only *L. longipes, L. bicolor,* and *L. proxima* are found commonly in *Sphagnum* bogs. *Laccaria trullissata* and *L. maritima* are found only in sand dunes or other very sandy areas, where they are putatively associated with species of *Pinus.*

Only *L. laccata* var. *pallidifolia, L. proxima,* and *L. tortilis* were found throughout the study range. *Laccaria bicolor* occurs in all areas except southeastern North America. All other taxa showed some geographical restriction. Taxa reported only from eastern North America are *L. amethystina, L. maritima, L. longipes, L. oblongospora, L. ochropurpurea, L. ohiensis, L. striatula, L. trichodermophora, L. trullissata,* and *L. vinaceobrunnea.* Conversely, *L. amethysteo-occidentalis, L. montana, L. nobilis,* and *L. pumila* have not been reported east of the Great Lakes region.

Phylogenetic Considerations

Placement of *Laccaria* in Ordinal and Family Treatments

A robust hypothesis of phylogenetic relationships for the Agaricales has not been developed. Several classifications have been advanced that reflect differences in views of relationships among genera in the group (e.g., Kühner, 1980; Jülich, 1981; Singer, 1986).

Kühner (1980, 1984) proposed dividing the Agaricales into several small orders that he felt were easier to define and had sharper boundaries than those traditionally recognized (e.g., Singer, 1975). He treated *Laccaria,* along with its gasteroid counterpart *Hydnangium,* as a separate family named the Hydnangiaceae within his order Tricholomatales (Kühner, 1980, 1984) (table 2). *Hydnangium* is the sister taxon to *Laccaria* and Tricholomataceae is the sister taxon to Hydnangiaceae in this classification.

TABLE 2. Placement of *Laccaria* in Kühner's (1980), Jülich's (1981), and Singer's (1986) classifications of agaricoid Hymenomycetes.

Kühner, 1980	Jülich, 1981	Singer, 1986
TRICHOLOMATALES	TRICHOLOMATALES	AGARICALES
Tricholomataceae	Hygrophoraceae	Tricholomataceae
Clitocybeae	Laccariaceae	Lyophylleae
Gerroneama, Omphalina, Arrhenia, Cantharellula, Clitocybe, Lepista, Ripartites, Armillaria	*Laccaria*	Termitomyceteae
Lyophylleae	Hydnangiaceae	Tricholomateae
Biannularieae	*Hydnangium*	Laccariinae
Tricholomeae	Fayodiaceae	*Laccaria*
Tricholomopsis, Leucopaxillus, Tricholoma, Pseudobaeospora, Melanoleuca	Collybiaceae	Clitocybinae
Cysterodermateae	Macrocystidiaceae	*Clitocybe, Lepista, Tricholomopsis*
Hydnangiaceae	Xerulaceae	Tricholomatinae
Laccaria, Hydnangium	Gigaspermaceae	*Tricholoma*
Rhodotaceae	Armillariaceae	Omphalinae
Pleurotaceae	Biannulariaceae	*Armillariella, Arthrosporella, Lulesia, Arrhenia, Leptoglossum, Omphalina, Gerronema, Callistosporium, Pleurocollybia, Lactocollybia, Macrocystidia, Fissolimbus, Asproinocybe*
Marasmiaceae	Tricholomataceae	Leucopaxilleae
Hygrophoraceae	Leucopaxillaceae	Biannularieae
Amanitaceae	Lyophyllaceae	Collybieae
	Marasmiaceae	Resupinateae
	Amparoinaceae	Panelleae
	Mycenaceae	Marasmieae
	Favolaschiaceae	Myceneae
	Nyctalidaceae	Pseudohiatulaeae
	Cyphellopsidaceae	Rhodoteae
	Lachnellaceae	
	Resupinataceae	
	Rhodotaceae	

Jülich (1981) also recognized the Tricholomatales as a separate order but treated *Laccaria* in his monotypic family Laccariaceae separate from, but closely related to, the Hydnangiaceae (table 2). These 2 families are among the 22 families that he recognized for the order (Jülich, 1981). Unfortunately, Jülich was not explicit on intraordinal relationships except to say that he did not recognize close relationships among many of these fungi. Thus, it is not clear what he thought was the sister group to the Laccariaceae and Hydnangiaceae.

Singer (1986) maintained that separation of the Agaricales into a number of smaller orders is not warranted. Within his classification, Singer (1986) placed *Laccaria* in a separate subtribe (Laccariinae) in Tribus Tricholomateae of the Tricholomataceae (table 2). Singer maintained that *Hydnangium,* as well as all other Gasteromycetes, is sufficiently distinct to prevent it from being treated in the Agaricales. Subtribe Clitocybinae is the sister taxon to *Laccaria* and Termitomyceteae is the sister taxon to Tricholomateae in this classification.

Molecular data obtained to date do not contain information with which the Agaricales *sensu* Singer can be divided into smaller orders. Rehner et al. (1990) reported that their sequence data of mitochondrial and nuclear ribosomal RNA genes do not resolve phylogenetic relationships within the Agaricales except to support the separation of the Boletales and the Russulales from the rest of the agarics. Lacking supportive evidence from molecular analyses, and heeding Singer's (1986) arguments for the use of caution regarding the multiplication and upgrading of higher taxa, I treat *Laccaria,* along with *Hydnangium* and *Podohydnangium* (see below), within the Tricholomataceae. It was beyond the scope of this study to try to resolve phylogenetic relationships within the Tricholomataceae. Until these relationships have been rigorously analyzed, I do not recognize infrafamiliar taxa in the Tricholomataceae. However, I accept Singer's (1986) and Kühner's (1980) view that *Laccaria* has closer affinities with genera in Singer's Tricholomateae and Kühner's Tricholomataceae than with other genera in the Tricholomataceae *sensu* Singer (1986).

Relationship of *Laccaria* to *Hydnangium* and *Podohydnangium*

Podohydnangium must be considered along with *Hydnangium* in discussions of the relationship of *Laccaria* to putative gasteroid relatives. *Podohydnangium* is a monotypic genus that differs from *Hydnangium* by having a distinct stipe-columella and, therefore, appears intermediate between *Laccaria* and *Hydnangium* (Beaton et al., 1984). *Podohydnangium* was not included in Kühner's (1980) and Jülich's (1981) treatments because it was first described in 1984, and it was excluded from Singer's (1986) classification for the same reason that he excluded *Hydnangium*: uncertainty of affinity.

The three classifications discussed above treat the relationship of *Laccaria* to *Hydnangium* and *Podohydnangium* differently (table 2). This is because of fundamental differences in opinion regarding the relationship of gasteroid genera to their agaric counterparts. Kühner (1980) and Jülich (1981) both treated certain gasteroid taxa within the Agaricales, incorporating them into the classification with their putative sister taxa. Singer (1986), on the other hand, maintained that the relationship of these fungi to epigeous agarics is not sufficiently resolved to justify incorporating them into the Agaricales.

Although *Laccaria, Podohydnangium,* and *Hydnangium* differ drastically in macromorphology, they share several presumably derived micromorphological character states, including identical basidiospore ornamentation and, at least in *Laccaria* and *Hydnangium* (*Podohydnangium* has not been examined), multinucleate basidiospores.

Laccaria is unique among epigeous agarics in that the conic echinulae, diagnostic features of the genus, are formed by microtubules that run perpendicular to the epispore (Besson & Kühner, 1971; Kühner, 1980; v. Hofsten & Mueller, unpubl.). SEM micrographs of basidiospores from *Podohydnangium australe* Beaton, Pegler & Young and several *Hydnangium* taxa have documented the similarity of shape of the basidiospore ornamentation between these taxa and *Laccaria* (Pegler & Young, 1979; Beaton et al., 1984; Castellano et al., 1989). Unpublished TEM data obtained by v. Hofsten (Institute of Physiological Botany, University of Uppsala, Uppsala, Sweden) documented that the basidiospore wall ultrastructure of *Hydnangium* is similar to that found in *Laccaria* (i.e., the echinulae are composed of microtubules that run perpendicular to the epispore).

All examined taxa of *Laccaria* as well as *Hydnangium carneum* have multinucleate basidiospores (table 1; Kühner, 1980; Tommerup et al., 1991).

The three genera also share several plesiomorphies such as having abundant clamp connections; having nonamyloid, acyanophilic basidiospores; and lacking a heteromerous trama (Pegler & Young, 1979; Beaton et al., 1984). Finally, *Podohydnangium australe* and at least some species of *Hydnangium* appear similar in color to orange-brown *Laccaria.*

The genera differ in that *Hydnangium* and *Podohydnangium* have statismosporic basidiospores that are orthotropic in development and *Laccaria* has ballistosporic basidiospores that are heterotropic in development. But, as pointed out by several authors (e.g., Pegler & Young, 1979; Beaton et al., 1984), *Hydnangium* is not closely related to any of the genera such as *Octavianina* O. Kuntze formerly treated in the polyphyletic Hymenogastrales *sensu* Singer and Smith (1960) and others.

Although *Laccaria, Hydnangium,* and *Podohydnangium* appear to form a monophyletic group, it is currently not possible to undertake a rigorous analysis of the relationship of these three genera to each other as no detailed systematic work has been carried out on either *Hydnangium* and *Podohydnangium* and species circumscriptions, composition, and relationships are still uncertain in these two genera. Castellano and Trappe (1990) accepted 23 names in *Hydnangium* in their bibliographic survey of Australian gasteroid fungi. Numerous systematic problems remain in the group, however, and some of these taxa probably belong in other genera. Until intra- and intergeneric relationships within this group are resolved, I choose to treat the taxa in this group as three separate genera (*Laccaria, Hydnangium, Podohydnangium*) in the Tricholomataceae *sensu* Singer (1986) amended to include *Hydnangium* and *Podohydnangium.* The inability to resolve infrafamiliar relationships within the family precludes recognizing the clade composed of these genera in a formal classification (see above).

Previously Published Infrageneric Classifications Proposed for *Laccaria*

Three primary infrageneric classifications have been proposed for *Laccaria* (Bon, 1983; Singer, 1986; Ballero & Contu, 1989) (table 3). Moser (1983), Clémençon (1984), and others have published variations of these classifications that do

TABLE 3. Primary infrageneric classifications proposed for *Laccaria*. Names in parentheses are the correct name for the taxon.

Bon, 1983	Singer, 1986	Ballero and Contu, 1989
Sect. *Maritimae* Bon	Stirps *Trullissata*	Sect. *Maritimae* Bon
L. trullissata	*L. trullissata*	*L. trullissata*
L. maritima	*L. maritima*	*L. maritima*
Sect. *Amethystinae* Bon	Stirps *Amethystina*	Sect. *Amethystinae* Bon
L. amethystina	*L. ochropurpurea*	*L. amethystea* (= *L. amethystina*)
L. bicolor	*L. bicolor*	*L. calospora* (= *L. amethystina*)
L. purpureobadia	*L. calospora* (= *L. amethystina*)	*L. violaceonigra*
Sect. *Laccata*	*L. amethystina* (= *L. amethysteo-occidentalis*)	*L. masonii*
Stirps *Ohiensis*	*L. lilacina*	*L. bicolor*
L. ohiensis (= *L. impolita*)	Stirps *Laccata*	*L. bullulifera*
L. tortilis	*L. laccata*	*L. farinacea* (= *L. trichodermophora*)
L. altaica (= *L. pumila*)	*L. farinacea* (= *L. trichodermophora*)	Sect. *Laccaria*
L. striatula (= ?)	*L. proximella*	Subsect. *Bisporae* Contu
L. lateritia (= *L. fraterna*)	*L. proxima*	*L. echinospora* (= *L. tortilis*)
Stirps *Laccata*	*L. tetraspora* (= *L. ohiensis*)	*L. singeri* (= *L. impolita*)
L. laccata	*L. montana*	*L. lateritia* (= *L. fraterna*)
L. affinis (= *L. laccata* var. *pallidifolia*)	*L. altaica* (= *L. pumila*)	*L. pumila*
Stirps *Tetraspora*	*L. echinospora* (= *L. tortilis*)	Subsect. *Laccaria*
L. proxima (= ?)	*L. fraterna*	*L. purpureobadia*
L. tetraspora (= *L. ohiensis*)	Stirps *Galerinoides*	*L. lutea* (= ?)
	L. galerinoides	*L. proxima*
	L. vinaceoavellanea	*L. montana*
	Stirps *Purpureobadia*	*L. laccata*
	L. purpureobadia	*L. tetraspora* (= *L. ohiensis*)
		L. affinis (= *L. laccata* var. *pallidifolia*)

not differ significantly from those presented in Table 3.

The primary difference between Bon's and Ballero and Contu's classification versus that of Singer's is the rank at which they recognized subgeneric taxa. Singer (1986) used the term stirps (a term not recognized by the International Code of Botanical Nomenclature, Greuter et al., 1988) rather than section to reflect the small hiatus between the subgeneric groups that he accepted. Bon (1983) and Ballero and Contu (1989) recognized three sections, with section *Laccaria* (incorrectly named *Laccata* by Bon, ICBN Art. 22.1, Greuter et al., 1988) being further divided into several subgroups. All three classifications recognized a separate group composed of *L. maritima* and *L. trullissata* and a group composed of *L. amethystina* and other taxa with violet to purple basidiomata (table 3). Bon (1983) and Ballero and Contu (1989) each recognized the species that have bisterigmate basidia as a separate subgroup. Singer (1986) included these taxa among species with tetrasterigmate basidia. He recognized stirps *Galerinoides* and *Purpureobadia* on differences in basidioma colors (Singer, 1986). Other differences between these three classifications (table 3) are due primarily to either varying interpretation of taxa or the inclusion of different taxa.

Cladistic Analyses

Cladistic analyses were undertaken to resolve infrageneric relationships within *Laccaria*. The infrageneric classifications of Bon (1983), Singer (1986), and Ballero and Contu (1989) discussed above were based on those authors' interpretations of the evolutionary history of the group. These authors, however, did not provide explicit statements regarding crucial assumptions and decisions used to develop their classifications. Without explicit information on choice and weighting of characters, character state evolution, homoplasy (convergence or parallelisms), and so forth, it is impossible to make an objective comparison or rigorously choose between these conflicting classifications.

Although cladistics has been used commonly in studies of plants and animals, such analyses have infrequently been used in fungal systematics. Cladistic methods are based on the theories first expounded by Hennig (1966), which have subsequently been expanded and modified by numerous workers (see reviews in Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Wiley, 1981; Duncan & Stuessy, 1984; Stuessy, 1990). The theoretical basis for these methods includes the following: (1) phylogenetic relationships are based on the idea of common ancestry (monophyly), (2) evidence for monophyletic groups (all, and only, the descendants of a particular ancestor) can only be determined by the detection of shared derived character states (synapomorphies), and (3) shared primitive character states (symplesiomorphies) do not provide evidence for relationships. Although there are operational and theoretical difficulties involved with any technique, cladistic analyses provide a rigorous method for making hypotheses of phylogenetic relationships.

Unfortunately, *Laccaria* does not lend itself to cladistic analysis. Problems in determining outgroups and in using the outgroup criterion for character state polarization are treated in the next subsection. Problems in choosing characters and in determining character state homology are also treated below. Care must be used, therefore, when interpreting the following results from the cladistic analyses. They are presented only as a working hypothesis of the evolutionary history of the genus, subject to revision.

Discussion of Choice of Outgroups—Lack of consensus regarding relationships within the Agaricales *sensu* Singer (1986) prevented me from making an unequivocal choice of an outgroup (see discussion at the beginning of this section and data in tables 2, 3). Uncertainty is not limited to the determination of the sister group to *Laccaria,* it also applies to the generic composition and circumscriptions of potential outgroups (Kühner, 1980, 1984; Singer, 1986).

The classifications presented in Table 2 propose conflicting hypotheses regarding the sister taxon to *Laccaria.* I used the entire Tricholomateae Singer, minus *Laccaria,* as the sister group to *Laccaria.* This group of taxa is roughly equivalent to the Clitocybeae plus Tricholomeae in Kühner's Tricholomataceae (Kühner, 1980, 1984). *Cantharellus* was used as the sister group to the Tricholomataceae. Although some workers do not derive the Tricholomataceae from a *Cantharellus*-like ancestor (e.g., Singer, 1986), I find this to be a plausible hypothesis, following the arguments of many workers (e.g., Petersen, 1971; Kühner, 1980, 1984; Bigelow, 1982).

It was well beyond the scope of this study to try to resolve relationships within the heterogeneous Tricholomateae. Instead, I divided the group into smaller units based only on characters shared by the outgroup and ingroup. Using this criterion I used the following operational units as outgroups: ***Cantharellus, Clitocybe, Lepista, Tricholomopsis* 1 & 2** (differing by basidiospore shape; represented by *Tricholomopsis flavissima* (Smith) Singer and *T. rutilians* (Schaeff.: Fr.) Singer, respectively), ***Tricholoma* 1 & 2** (differing by basidiospore shape; represented by *Tricholoma aurantium* (Fr.) Rick-en and *T. michiganense* Smith, respectively), **Omphalinae 1 & 2** (differing by basidiospore shape; represented by *Omphalina hepatica* (Fr.) Orton and *Leptoglossum rickenii* (Hora) Singer, respectively), and **Omphalinae 3-5** (differing by the number of sterigmata per basidium and number of nuclei per basidiospore; represented by *Gerroneama chrysophyllum* (Fr.) Singer, *Omphalina pseudoandrosacea* (Bull.) Moser, and *O. griseopallida* (Desm.) Quél., respectively) (table 5). For ingroups, I used all of the *Laccaria* taxa recognized from the continental United States and Canada. I further divided *L. laccata* into three groups, ***L. lac* 1-3** (differing in basidiospore shape), because of the high degree of plasticity observed in this character in this taxon. Extralimital taxa were not included in these analyses because of a lack of information on somatic culture mat morphology and difficulties in interpreting the macromorphology, especially color, for a number of taxa that I know only from the literature and from an examination of their type specimens.

Another serious problem in determining suitable taxa to use as outgroups to *Laccaria* is that many of the systematically informative characters in *Laccaria* do not occur in prospective outgroups (e.g., length and width of basidiospore echinulae and, as coded, basidioma and culture mat pigments). It also was impossible to determine character state homology for characters such as basidioma and basidiospore size between putative outgroups and *Laccaria* taxa. Because of these problems, only 5 of the 14 characters employed in the final analyses could be coded for both the outgroups and ingroups (tables 4, 5). Thus, most of the ingroup characters could not be polarized directly by outgroup comparison (Watrous & Wheeler, 1981; Maddison et al., 1984).

Three separate sets of analyses were run. First,

TABLE 4. Characters and their states used in cladistic analyses.

1. Number of sterigmata per basidium. 0 = 4; 1 = 2, 3; 2 = 5–8
2. Number of nuclei/basidiospore. 0 = 1; 1 = multiple
3. Echinulate basidiospores with echinulae formed by perpendicular microtubules. 0 = absent; 1 = present
4. Mean echinulae length (in μm). 0 = rugulose; 1 = < 0.5; 2 = 0.5–1; 3 = 1–2; 4 = > 2
5. Echinulae base width (in μm). 0 = $\leq$ 1; 1 = $\geq$ 1.2
6. Mean basidiospore length. 0 = short (< 8 μm); 1 = moderate (8–10 μm); 2 = long (10–13 μm); 3 = elongate (> 13.5 μm)
7. Basidiospore shape ($\bar{Q}$). 0 = globose ($\bar{Q}$ = 1–1.05); 1 = subglobose to broadly ellipsoid ($\bar{Q}$ = 1.06–1.23); 2 = ellipsoid ($\bar{Q}$ = 1.24–1.6); 3 = oblong ($\bar{Q}$ = 1.65–2); 4 = cylindrical or fusiform ($\bar{Q}$ > 2)
8. Cheilocystidia shape. 0 = absent or filamentous and not strongly morphologically differentiated; 1 = subclavate to clavate; 2 = very large and inflated
9. Pileus color when young and fresh. 0 = flesh color to orange-brown; 1 = violaceous; 2 = red-brown; 3 = violet-brown; 4 = ochraceous; 5 = rust
10. Lamellar color when young and fresh. 0 = flesh color; 1 = vinaceous; 2 = violet to purple; 3 = rose pink
11. Basal mycelium color when young and fresh. 0 = white; 1 = violet
12. Pileus size. 0 = moderate; 1 = small; 2 = large
13. Stature. 0 = moderate; 1 = gracile; 2 = robust
14. Color of somatic culture mat on PDA and MMN. 0 = white to olive brown; 1 = violet

outgroup and ingroup relationships were examined using the five shared characters (fig. 3). Second, resolution of ingroup relationships was attempted using all available characters for the ingroup without the outgroups. This resulted in the unrooted network presented in Figure 4. Finally, to develop an operational classification, analyses of the combined data set were run to identify functional outgroups within *Laccaria* (Watrous & Wheeler, 1981), thereby constraining possible tree topologies (fig. 5).

DISCUSSION OF CHARACTERS AND CHARACTER STATE ASSIGNMENTS—Table 4 lists the characters and their states used in these analyses. Other characters (e.g., presence or absence of striations, pileus texture, growth rate of cultures on various media, etc.) were employed in preliminary analyses but were subsequently deleted for various reasons, including a high degree of variability of such characters within and among taxa or their autapomorphic nature (i.e., they varied only in one terminal taxon and thus did not provide information on relationships among taxa). Size character (nos. 6, 17, and 18) were coded only for ingroup taxa because of the impossibility of estimating homology with states in the outgroups. Color characters (nos. 11, 12, 13, and 19) were limited to ingroup taxa for the same reason. To my knowledge, the identity and structure of the pigments in *Laccaria* are unknown (see Discussion of Systematic Characters). Thus, it is not possible to determine homology of pigments observed in *Laccaria* with those found in other genera with orange-brown and violet pigments. Lack of knowledge of the pigments in *Laccaria* causes problems in ingroup as well as outgroup analyses. I have made the assumption that the violet coloration observed in many *Laccaria,* from the lamellae and stipe basal mycelium in *L. bicolor* to the entire basidioma in *L. amethystina,* is due to the same pigment(s).

Information on number of sterigmata per basidium and number of nuclei per basidiospore (characters 1 and 2, respectively; table 4) for outgroups was obtained from a number of sources including Corner (1966), Kühner (1980, 1984), Bigelow (1982), and Singer (1986).

PRELIMINARY HYPOTHESIS OF PHYLOGENETIC RELATIONSHIPS BASED ON CLADISTIC ANALYSES—Analyses undertaken for this study were performed using PAUP Version 3.0L (Swofford, 1989) running on a MAC II ci. All multistate characters were interpreted as unordered because I could not make *a priori* decisions on character state transformation series. The number of taxa included in the analyses precluded the use of exact methods to find the shortest trees, so a heuristic method using branch swapping (tree bisection–reconnection) was employed to search for optimum trees. The MULPARS option was invoked to save 300 equally most parsimonious trees. A shorter tree was sometimes located even after 200 trees were saved. Ten replications using random addition sequences were employed to ensure that addition sequence did not affect tree length or topology. Characters and their states employed in the final sets of analyses are listed in Tables 4 and 5.

A strict consensus tree of the 300 most parsimonious trees saved in the analysis restricted to the characters that could be coded for both ingroups and outgroups is presented in Figure 3. This tree has a length of 28 steps with a homoplasy index (HI) of 0.643 and a rescaled consistency index (RC) of 0.211. While ingroup relationships were not resolved in this analysis, *Laccaria* formed a monophyletic clade apart from the outgroup taxa that was supported by one synapomorphy, basidiospore echinulae ultrastructure (character 3).

Only five characters could be used in this analysis (table 4, characters 1–3, 7, and 8) and of these

TABLE 5. Taxon by character state matrix used in cladistic analyses. Characters and character states are provided in Table 4. Outgroups employed were *Cantharellus* and species of Singer's (1986) Tricholomataceae excluding *Laccaria* (table 2).

Taxon	Character number													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Canth (*Cantharellus*)	2	0	0	?	?	?	2	0	?	?	?	?	?	?
Clito (*Clitocybe*)	0	0	0	?	?	?	2	0	?	?	?	?	?	?
Lepist (*Lepista*)	0	0	0	?	?	?	2	0	?	?	?	?	?	?
Tmopsis 1 (*Tricholomopsis* 1)	0	0	0	?	?	?	0	2	?	?	?	?	?	?
Tmopsis 2 (*Tricholomopsis* 2)	0	0	0	?	?	?	2	2	?	?	?	?	?	?
Trich 1 (*Tricholoma* 1)	0	0	0	?	?	?	1	0	?	?	?	?	?	?
Trich 2 (*Tricholoma* 2)	0	0	0	?	?	?	2	0	?	?	?	?	?	?
Omphal 1 (Omphalinae 1)	0	0	0	?	?	?	1	0	?	?	?	?	?	?
Omphal 2 (Omphalinae 2)	0	0	0	?	?	?	2	0	?	?	?	?	?	?
Omphal 3 (Omphalinae 3)	0	1	0	?	?	?	2	0	?	?	?	?	?	?
Omphal 4 (Omphalinae 4)	1	0	0	?	?	?	2	0	?	?	?	?	?	?
Omphal 5 (Omphalinae 5)	1	1	0	?	?	?	2	0	?	?	?	?	?	?
L. a-o (*amethysteo-occidentalis*)	0	1	1	3	0	1	1	1	1	2	1	2	0	1
L. ame (*amethystina*)	0	1	1	3	1	1	0	1	1	2	1	0	0	1
L. bic (*bicolor*)	0	1	1	3	0	0	1	0	0	1	1	0	0	1
L. frat (*fraterna*)	1	1	1	3	0	2	1	0	5	3	0	0	0	0
L. lac 1 (*laccata* 1)	0	1	1	3	0	1	0	0	0	0	0	0	0	0
L. lac 2 (*laccata* 2)	0	1	1	3	0	1	1	0	0	0	0	0	0	0
L. lac 3 (*laccata* 3)	0	1	1	3	0	1	2	0	0	0	0	0	0	0
L. long (*longipes*)	0	1	1	3	0	0	1	0	0	0	0	0	0	0
L. mar (*maritima*)	0	1	1	1	0	3	3	0	2	2	1	0	2	?
L. mont (*montana*)	0	1	1	3	0	2	1	0	0	0	0	1	1	0
L. nob (*nobilis*)	0	1	1	3	0	0	1	0	0	1	1	2	2	1
L. obl (*oblongospora*)	0	1	1	2	0	1	2	0	0	0	1	0	0	1
L. och (*ochropurpurea*)	0	1	1	3	0	1	0	0	4	2	1	2	2	1
L. ohi (*ohiensis*)	0	1	1	4	1	1	0	0	0	0	0	1	1	0
L. pro (*proxima*)	0	1	1	2	0	1	2	0	0	0	0	0	0	0
L. pum (*pumila*)	1	1	1	3	0	2	1	0	0	0	0	1	1	0
L. stri (*striatula*)	0	1	1	4	1	1	0	0	0	0	0	0	1	0
L. tort (*tortilis*)	1	1	1	4	1	2	0	0	0	0	0	1	1	?
L. tric (*trichodermophora*)	0	1	1	3	0	0	1	0	0	0	1	0	0	1
L. trul (*trullissata*)	0	1	1	0	0	3	4	0	1	2	1	2	2	1
L. v-b (*vinaceobrunnea*)	0	1	1	3	0	1	1	1	3	2	1	0	0	1

only characters 3 (presence or absence of echinulate basidiospores) and 8 (cheilocystidia shape) were not homoplasious. Character 3 is the synapomorphy supporting the *Laccaria* clade; character 8 occurs in 3 states. Although most taxa lack or have filamentous cheilocystidia (state 0), inflated cheilocystidia can be found in two of the outgroups. *Laccaria amethysteo-occidentalis, L. amethystina,* and *L. vinaceobrunnea* have clavate cheilocystidia.

The distribution of multinucleate basidiospores (character 2) along this tree is significant because Kühner (1980, 1984) emphasized the occurrence of multinucleate basidiospores in *Laccaria* in his rationale for recognizing the genus as a family separate from other genera typically treated in the Tricholomataceae (table 2). Although *Laccaria* is characterized by having multinucleate basidiospores, this character state is also present in two of the outgroup taxa (character 2, fig. 3). Until the phylogeny of the outgroup (Singer's Tricholomataceae excluding *Laccaria*) is elucidated, it is impossible to determine whether the presence of multinucleate basidiospores is symplesiomorphic or was derived independently in two or more clades within the Tricholomataceae.

Figure 4 presents the results of the analysis of ingroup relationships utilizing all of the characters listed in Table 4 (minus characters 2 and 3 because they were uninformative for ingroup comparisons). The strict consensus tree of the 300 most parsimonious trees saved is presented as an unrooted network because no outgroup was used to root the tree. The network (fig. 4) has a length of

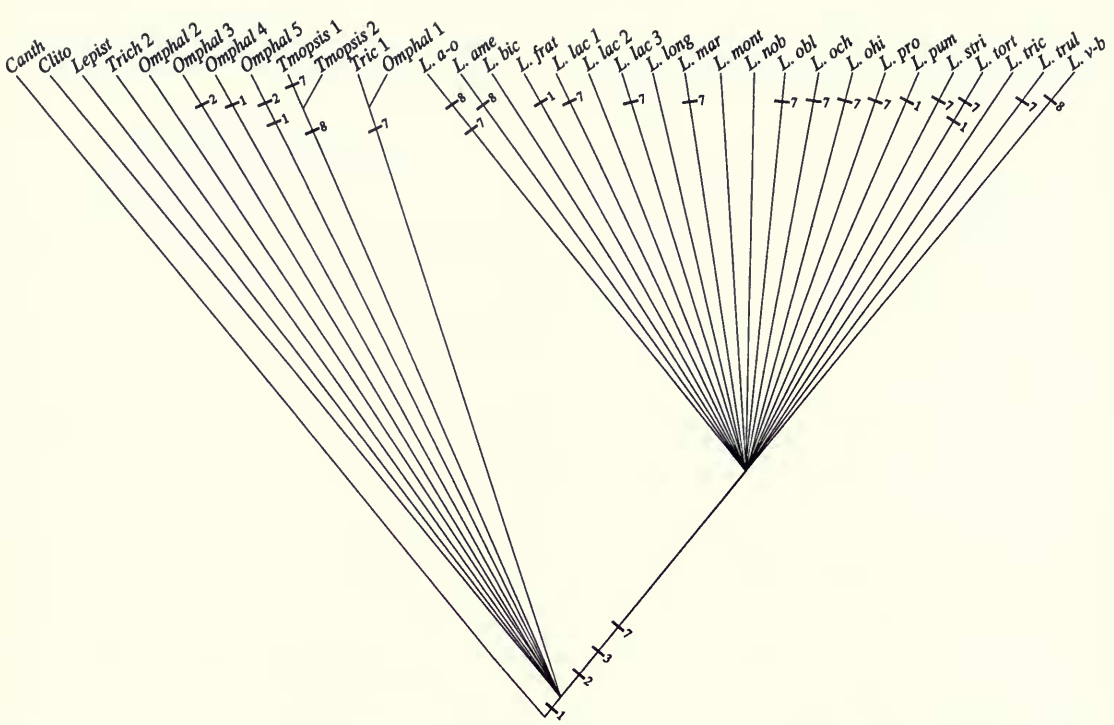


FIG. 3. Strict consensus tree resulting from analyses restricted to characters shared by ingroup and outgroup taxa (characters 1–3, 7, and 8 in table 4). Only characters 3 and 8 were not homoplasious. Length 28, HI = 0.643, RC = 0.211. Refer to Table 5 for abbreviations.

51 steps, a consistency index (CI) of 0.549, and an RC of 0.345. Only select characters were traced onto the network illustrated in Figure 4. All characters are mapped along the tree presented in Figure 5 (analysis of combined outgroup and ingroup data).

All characters except echinulae length (character 4), cheilocystidia (character 8), pileus color (character 9), and color of lamellae (character 10) were homoplasious. Because of this high level of homoplasy, the network is not fully resolved and not robust. The addition or deletion of a character or a change in coding of the states of one character had a profound impact on network topology.

Several subgroups within *Laccaria* were resolved during these analyses (fig. 4). *Laccaria*

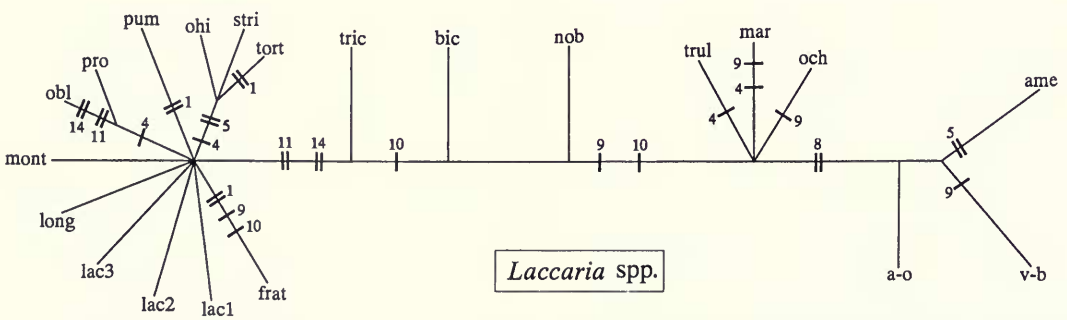


FIG. 4. Unrooted network (strict consensus of 300 trees) of ingroup relationships. All characters except 2 and 3 (uninformative) listed in Table 4 were employed. Characters 4, 8, 9, and 10 were not homoplasious. Only select characters were traced onto the network. Length 51, HI = 0.549, RC = 0.345. Refer to Table 5 for abbreviations.

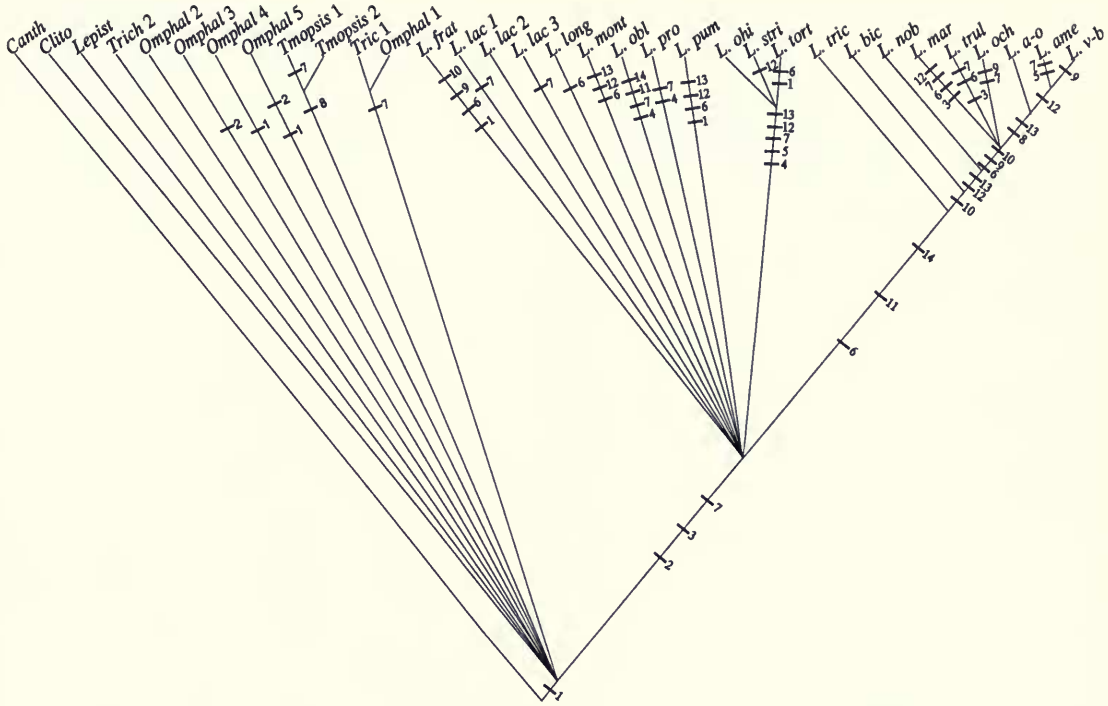


FIG. 5. Strict consensus cladogram using all characters listed in Table 4 showing one possible resolution of where to root the network presented in Figure 4. Only characters 4, 8, 9, and 10 were not homoplasious. Refer to Table 5 for abbreviations.

ohiensis, L. striatula, and *L. tortilis* formed a trichotomy separate from the other North American taxa that lack violet pigments (fig. 4). This clade was supported by the presence of strongly echinulate, globose basidiospores (characters 4, 5, and 7) and small gracile basidiomata (characters 12 and 13). *Laccaria proxima* and *L. oblongospora* formed a clade supported by the presence of finely echinulate basidiospores (state 2, character 4). These two clades, along with the other taxa that lack violet basidioma pigments, formed an unresolved "bush" separate from taxa with violet basidioma pigments. Resolution was higher within the North American taxa with violet pigments. This grade was supported by the presence of violet mycelium at the stipe base and violet culture mats on PDA and MMN media (characters 11 and 14). Both of these states, however, occur also in *L. oblongospora,* which was not placed in this grade. The *L. bicolor* complex (i.e., *L. trichodermophora, L. nobilis,* and *L. bicolor*) was fully resolved and formed a sister group to the taxa with violet to purple lamellae. *Laccaria trullissata* and *L. maritima* formed a trichotomy with *L. ochropurpurea* owing to their large basidioma size and stature (characters 12 and 13) and similarity in coloration (characters 9–11). The clade composed of *L. amethysteo-occidentalis, L. amethystina,* and *L. vinaceobrunnea* was supported by the presence of large cheilocystidia (character 8).

The distribution of violet basal mycelium and violet somatic culture mats on PDA and MMN media (state 1 of characters 11 and 14, respectively) along this network causes difficulties in interpreting character state changes throughout *Laccaria.* Based on the topology of the network, violet pigments occur in two places along the tree: in *L. oblongospora* and in the grade that includes *L. trichodermophora–L. vinaceobrunnea.* It is impossible to determine which is the plesiomorphic state for these two characters. The occurrence of these states in two areas of the tree could be due either to a parallel gain of pigment(s), a reversal back to the plesiomorphic state, or the incorrect placement of *L. oblongospora.* This is a serious weakness in these results because, as discussed below, the major subgroups identified through these analyses are supported by pigment composition and their distribution.

Based on these analyses, bisterigmate basidia

(state 1, character 1) arose independently three times within the North American taxa of *Laccaria*: in *L. fraterna, L. pumila,* and *L. tortilis.*

Laccaria laccata was divided into three operational taxa in these analyses because of plasticity of basidiospore shape within individuals referable to *L. laccata* on the basis of other character states. These analyses were uninformative for resolving at what rank to recognize these morphological forms of *L. laccata.*

The data sets (all characters for both ingroup and outgroup taxa) were combined in an effort to constrain the choice of a functional outgroup and provide an operational classification based on a tentative hypothesis of relationships among the ingroup taxa. Because only five characters were shared by the ingroup and outgroup, the results of this analysis provide only one of the possible resolutions of where to root the network presented in Figure 4. Figure 5 shows the results of this analysis. The resulting strict consensus tree of the 300 most parsimonious trees saved was 64 steps long and had a CI of 0.500 and an RC of 0.332.

The unresolved group composed of the taxa lacking violet basidioma pigments plus *L. oblongospora* is basal on this tree (fig. 5). The only difference in ingroup topology between this tree and the unrooted network (fig. 4) is that *L. oblongospora* and *L. proxima* are not placed together in a separate clade.

Proposed Operational Classification of *Laccaria*

The classification used in this monograph is based on an attempt to rigorously analyze all available data using cladistic methods. The employed data set included data on macro- and micromorphology of basidiomata and somatic culture mats, cytology, and basidiospore wall ultrastructure.

Two major subgroups within the North American taxa of *Laccaria* were identified in these analyses (figs. 4, 5). One subgroup consists of all taxa lacking violet basidioma pigments plus *L. oblongospora*; the second subgroup consists of the remaining taxa possessing violet basidioma pigments. Although these two subgroups are clearly separated on the cladograms, they are not supported by any synapomorphies. No characters, plesiomorphic or apomorphic, support recognition of the taxa composing the basal group as a monophyletic group separate from the rest of the ingroup taxa. Additionally, although the grade consisting of *L. trichodermophora* through *L. vinaceobrunnea* appears well supported by the presence of violet mycelium at the stipe base and by violet culture mats on PDA and MMN media, these character states also occur in *L. oblongospora* and therefore are present in the other main subgroup. Taxa need to be based on the occurrence of unique sets of derived characters, and thus these two subgroups should not be formally recognized.

The concept of metataxa has been proposed as a means of recognizing unresolved groups (e.g., Donoghue, 1985; de Queiroz & Donoghue, 1988). Because data do not exist to refute their monophyly, the two subgroups are treated as metasections in this monograph, metasections *Laccaria* and *Amethystina.* Metasection *Amethystina* is supported by two character state changes: the presence of violet mycelium at the stipe base, and violet somatic mats on PDA and MMN media. Metasections were used in this treatment, even though metataxa have been criticized by a number of authors (e.g., Kluge, 1989; Nixon & Wheeler, 1990; de Queiroz & Gauthier, 1990), to provide an operational classification and a testable hypothesis of relationships within *Laccaria.*

Although taxa in metasection *Amethystina* are almost fully resolved, only the clade consisting of *L. amethysteo-occidentalis, L. amethystina,* and *L. vinaceobrunnea* is supported by a synapomorphy: the presence of large, clavate cheilocystidia (figs. 4, 5). For this reason, metasection *Amethystina* is not further divided. Similarly, no subgroups are recognized within metasection *Laccaria.*

This classification differs from previously published classifications (table 3) by the recognition of fewer subgeneric groups. The three classifications presented in Table 3 all recognized a separate group, either section or stirps, for *L. trullissata* and *L. maritima.* These two taxa formed a trichotomy with *L. ochropurpurea* in the cladistic analysis (figs. 4, 5) and could not be recognized as a separate monophyletic group.

The results of these analyses are in conflict with the hypothesis that the *Laccaria* species characterized by bisterigmate basidia compose a monophyletic group separate from tetrasterigmate taxa. Bon's (1983) stirps *Ohiensis* and Ballero and Contu's (1989) subsection *Bisporae* are paraphyletic according to my analyses and therefore are not recognized.

The tree topology shown in Figures 4 and 5 is concordant with the results obtained to date on relationships based on molecular data. Analyses

of RFLPs of mtDNA (Gardes et al., 1991a) indicated that *L. laccata* var. *pallidifolia* was phenetically more similar to the *L. bicolor* complex than *L. proxima* was to the *L. bicolor* complex. The employed isolates of *L. amethystina* were phenetically distant, based on mtDNA RFLPs from all of these taxa (Gardes et al., 1991a). Similarly, Gardes and colleagues (Gardes et al., 1991b) reported that sequence variation in the internal transcribed spacer (ITS) of the nuclear ribosomal repeat unit was less between the one tested isolate of *L. laccata* var. *pallidifolia* and the three tested isolates of *L. bicolor sensu lato* than between *L. proxima* and the *L. bicolor* complex. Although these data do not resolve the issue of where to root the network presented in Figure 4, they are concordant with placing *L. proxima, L. laccata,* and taxa in the *L. bicolor* complex in a linear series.

These conclusions are summarized below in the Conspectus of North American Taxa.

Conspectus of North American Taxa

AGARICALES, TRICHOLOMATACEAE
- Metasection *Laccaria*
  - *Laccaria proxima*
  - *Laccaria oblongospora*
  - *Laccaria laccata* var. *laccata*
  - *Laccaria laccata* var. *pallidifolia*
  - *Laccaria longipes*
  - *Laccaria fraterna*
  - *Laccaria montana*
  - *Laccaria pumila*
  - *Laccaria striatula*
  - *Laccaria ohiensis*
  - *Laccaria tortilis*
- Metasection *Amethystina*
  - *Laccaria trichodermophora*
  - *Laccaria bicolor*
  - *Laccaria nobilis*
  - *Laccaria trullissata*
  - *Laccaria maritima*
  - *Laccaria ochropurpurea*
  - *Laccaria amethysteo-occidentalis*
  - *Laccaria amethystina*
  - *Laccaria vinaceobrunnea*

North American Taxa

Laccaria Berkeley & Broome, Ann. Mag. Nat. Hist. 12: 370. 1883.

≡ *Russuliopsis* Schroeter, Die Pilze Schlesiens: 622–623. 1889.

Pileus convex to plane, glabrous, finely fibrillose to fibrillose-scaly or scaly to squarrose, astriate to plicate-striate or pellucid-striate, hygrophanous, orange-brown, ochraceous, pinkish flesh color, dark violaceous, vinaceous, rusty red-brown, gray-black, or fawn; lamellae sinuate to subdecurrent, close to distant, thick, waxy appearing, narrow to broad, light flesh pink color, vinaceous, violaceous, rose pink or ash gray; stipe equal to subclavate, glabrous to coarsely fibrillose, often longitudinally striate; basal mycelium white or violet; basidiospores in mass white, rarely light violet; pileipellis morphologically undifferentiated with interwoven hyphae, or fasciculate, or a trichodermium; basidia 2- or 4-sterigmate, clavate; pleurocystidia rare; cheilocystidia absent to abundant, filamentous and morphologically undifferentiated to clavate or subcapitate; basidiospores globose to oblong and echinulate or elongate and finely roughened, multinucleate; echinulae composed of microtubules that run perpendicular to epispore; clamp connections at nearly all septa; basidiospores and all elements inamyloid, not dextrinoid, acyanophilic. Terrestrial, cosmopolitan.

Key to *Laccaria* Occurring in North America North of Mexico

1. Lamellae violaceous to purple when young and fresh 2
1. Lamellae flesh color to pinkish when fresh 10
   2. Basidiospores 13.5–22 × 5.5–9.5 μm, elongate, smooth to finely roughened or very finely echinulate (echinulae < 0.5 μm long); in sand or very sandy soil; north central and eastern North America 3
   2. Basidiospores < 10.5 μm long, less elongate ($\bar{Q} \leq 1.5$), echinulae > 0.5 μm long; in sand or not in sand 4
3. Basidiospores subfusiform ($\bar{Q} = 2.4$–2.5), not echinulate, appearing finely roughened on SEM; eastern and midwestern North America ..... *L. trullissata* (p. 64)

3. Basidiospores oblong ($\bar{Q}$ = 1.7–1.8); finely echinulate (echinulae 0.2–0.5 μm long); Europe, only few Canadian collections known ..... *L. maritima* (p. 65)
4. Pileus and stipe bright violaceous or purple when young and fresh; cheilocystidia large (up to 92 × 12 μm), clavate, abundant 5
4. Pileus and stipe orange-brown, pinkish flesh color, wine color, avellaneous, or buff color; cheilocystidia smaller, filamentous, common to absent 7
5. Basidiospores globose, echinulae > 1 μm wide at base; basidiomata fading from amethyst to grayish then buff in age; eastern North America ..... *L. amethystina* (p. 71)
5. Basidiospores subglobose to broadly ellipsoid; echinulae ≤ 1 μm wide at base; basidiomata changing from amethyst to vinaceous or reddish brown; eastern or western North America 6
6. Basidiomata large (pilei 10–90 mm diam.), amethyst, becoming vinaceous; pileipellis hyphae interwoven with scattered fascicles of perpendicular hyphae; western North America; under conifers ..... *L. amethysteo-occidentalis* (p. 69)
6. Basidiomata smaller (pilei 7–25[–45] mm diam.); amethyst, becoming reddish brown; pileipellis hyphae interwoven with numerous, large, individual perpendicular hyphae; Gulf Coast states; under *Quercus* ..... *L. vinaceobrunnea* (p. 72)
7. Lamellae dark purple, thick, waxy appearing; basidiomata large (pilei up to 60–120 mm diam.), violaceous buff when young and fresh, becoming buff; basidiospores globose to subglobose, echinulae 1–1.5 μm wide at base; eastern North America ..... *L. ochropurpurea* (p. 67)
7. Lamellae light vinaceous, not thick or waxy appearing; basidiomata moderate to large (pilei up to 85 mm diam.), pinkish flesh color when fresh or vinaceous; basidiospores subglobose to broadly ellipsoid or ellipsoid to oblong, echinulae < 1.2 μm long and ≤ 1 μm wide at base; eastern and western North America 8
8. Basidiomata vinaceous to avellaneous; basidiospores ellipsoid to oblong ($\bar{Q}$ = 1.4–1.6); echinulae ≤ 0.5 μm long; southern Mississippi and Texas ..... *L. oblongospora* (p. 30)
8. Basidiomata pinkish flesh color to reddish brown; basidiospores subglobose to broadly ellipsoid, $\bar{x}$ < 8.5 μm long; widely distributed 9
9. Pileus 16–85 mm diam., often strongly scaly to squarrose; stipe large and robust (26–110[–160] × 4–10[–16] mm), strongly striate to reticulate; western North America and upper Great Lakes region, not commonly encountered ..... *L. nobilis* (p. 61)
9. Pileus 8–50(–70) mm diam., finely fibrillose to minutely scaly; stipe smaller (23–85[–130] × 3–6 [–10] mm) and not strongly striate; western North America and upper Great Lakes region, commonly encountered ..... *L. bicolor* (p. 57)
10. Basidia (3-)4-sterigmate 11
10. Basidia 2(-3)-sterigmate 22
11. Basidiospore echinulae < 1 μm long; basidiospores broadly ellipsoid to oblong ($\bar{Q}$ = 1.25–1.6) 12
11. Basidiospore echinulae ≥ 1 μm long; basidiospores globose to ellipsoid 13
12. Basidiospores $\bar{x}$ = 8.3–9.0 × 5.6–6 μm, oblong ($\bar{Q}$ = 1.45–1.6); mycelium at stipe base violet, fading white; Gulf Coast states ..... *L. oblongospora* (p. 30)
12. Basidiospores $\bar{x}$ = 9–11.5 × 6.7–8(–8.8) μm, ellipsoid ($\bar{Q}$ = 1.25–1.35[–1.4]); mycelium at stipe base white; widely distributed ..... *L. proxima* (p. 27)
13. Mycelium at stipe base violaceous when fresh, becoming white with age; basidiospores small ($\bar{x}$ = 7–8.4[–9] × 6–8 μm) 14
13. Mycelium at stipe base white from onset; basidiospores larger ($\bar{x}$ = 8.2–13 μm long) (but see no. 20, *L. longipes*) 16
14. Lamellae flesh-colored to pinkish flesh color; basal mycelium scant, strongly hygrophanous; basidiomata orange-brown; pileipellis a trichodermium or of interwoven hyphae with numerous large fascicles of perpendicular hyphae; southeastern North America ..... *L. trichodermophora* (p. 55)
14. Lamellae light vinaceous, occasionally fading to pinkish color; basal mycelium copious, basidiomata pinkish flesh color to reddish brown; pileipellis hyphae interwoven with scattered fascicles of perpendicular hyphae; western North America to Ontario and Michigan 15
15. Pileus 16–85 mm diam., strongly scaly to squarrose; stipe large and robust (26–110[–160] × 4–10

[–16] mm), strongly striate to reticulate; western North America and upper Great Lakes region, not commonly encountered ..... *L. nobilis* (p. 61)

15. Pileus 8–50(–70) mm diam., finely fibrillose to minutely scaly; stipe smaller (23–85[–130] × 3–6 [–10] mm) and not strongly striate; western North America and upper Great Lakes region, commonly encountered ..... *L. bicolor* (p. 57)
    16. Basidiospores relatively large ($\bar{x}$ = 9.4–12.6 × 8.5–10.5 μm); pilei up to 35 mm broad, striate to (often) strongly striate; restricted to arctic, boreal, or alpine habitats .. *L. montana* (p. 42)
    16. Basidiospores smaller; pilei small to large, not striate or occasionally finely striate, some translucent-striate 17
17. Pileus 16–85 mm diam., strongly scaly to squarrose; stipe large and robust (26–110[–160] × 4–10 [–16] mm), strongly striate to reticulate ..... *L. nobilis* (p. 61)
17. Pileus smaller (5–45[–60] mm diam.), glabrous to finely scaly; stipe smaller, not strongly striate 18
    18. Basidiospores globose; echinulae > 1.5 μm long, > 1.2 μm wide at base 19
    18. Basidiospores globose to ellipsoid; echinulae 0.7–2 μm long, ≤ 1 μm wide at base 20
19. Stipe 20–70(–103) × 1–4 mm, darker than pileus; in moist areas, often among mosses (not *Sphagnum*); eastern North America, commonly encountered ..... *L. striatula* (p. 46)
19. Stipe 12–25(–40) × 1–2 mm, concolorous with pileus; cosmopolitan, not commonly encountered in north temperate regions ..... *L. ohiensis* (p. 48)
    20. Basidiospores small ($\bar{x}$ = 7.6–7.8 × 6.8–7.2 μm); pilei strongly translucent-striate; stipes long (67–138[–165] mm); growing among mosses, especially *Sphagnum*, usually in bogs, northeastern North America and upper Great Lakes region ..... *L. longipes* (p. 38)
    20. Basidiospores larger ($\bar{x}$ > 8 μm long); pileus not striate, striate or slightly translucent-striate; stipe shorter; growing among mosses or not, not normally found in bogs; widely distributed 21
21. Basidiospores broadly ellipsoid to ellipsoid ($\bar{Q}$ = 1.2–1.3); rarely encountered ..... *L. laccata* var. *laccata* (p. 34)
21. Basidiospores globose to broadly ellipsoid ($\bar{Q}$ = 1–1.5[–2]); commonly encountered, widely distributed ..... *L. laccata* var. *pallidifolia* (p. 35)
    22. Basidiospores usually < 11 μm long; basidiomata rusty red-brown; under *Eucalyptus* ..... *L. fraterna* (p. 39)
    22. Basidiospores > 11 μm long; under native North American trees 23
23. Basidiospores 11–17 × 10–14.5 μm, subglobose to broadly ellipsoid ($\bar{Q}$ = 1.1–1.2); echinulae < 1.5 μm long; montane, boreal, or arctic habitats ..... *L. pumila* (p. 44)
23. Basidiospores 10–15 × 10–15 μm, globose; echinulae > 2 μm long; temperate habitats ..... *L. tortilis* (p. 50)

Laccaria Metasection Laccaria
[see p. 24 for discussion]

Basidiomata and somatic culture mats lacking violet pigment(s), or violet pigment(s) present and basidiospores ellipsoid and finely ornamented (echinulae 0.5–1 μm long).

Laccaria proxima (Boudier) Patouillard. Figures 6–8, 53a,b, 69c.

≡ *Clitocybe proxima* Boudier, Bull. Soc. Bot. France 28: 91. 1881. TYPE: Plate II, fig. 2 in Boudier, Bull. Soc. Bot. France 28. 1881 (lectotype, *fide* Mueller, 1991a). Representative specimen: France, Montemorency, November 1904, *Boudier s.n.* (as *C. proxima*) (PC!, "neotype" *fide* Mueller, 1987).
≡ *Laccaria proxima* (Boudier) Patouillard, Hymeno. Eur.: 97. 1887.
≡ *Laccaria laccata* var. *proxima* (Boudier) Maire, Bull. Soc. Mycol. France 24: 16. 1908.
≡ *Clitocybe laccata* var. *proxima* (Boudier) Bresadola. Icon. Mycologica: 43. 1927.

MACROMORPHOLOGY—**Pileus** (7–)15–69(–83) mm broad, campanulate to convex, often becoming plane to uplifted, some depressed, not striate, occasionally translucent-striate when faded, finely fibrillose to fibrillose, some becoming fibrillose-scaly to scaly or squarrose in age, hygrophanous, reddish brown to orange-brown ("Auburn," "Sanford's Brown," "Orange Rufous," "Hazel," "Cinnamon-Rufous"), fading lighter ("Apricot Buff");

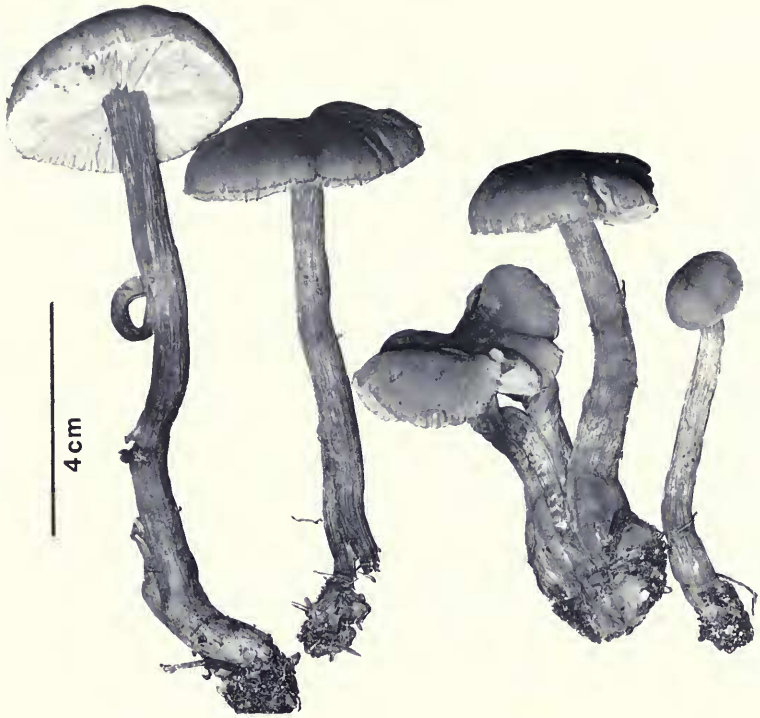


FIG. 6. Basidiomata of *L. proxima* (GMM 2100).

FIG. 7. Somatic culture mats of *L. proxima* (GMM 1518). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.

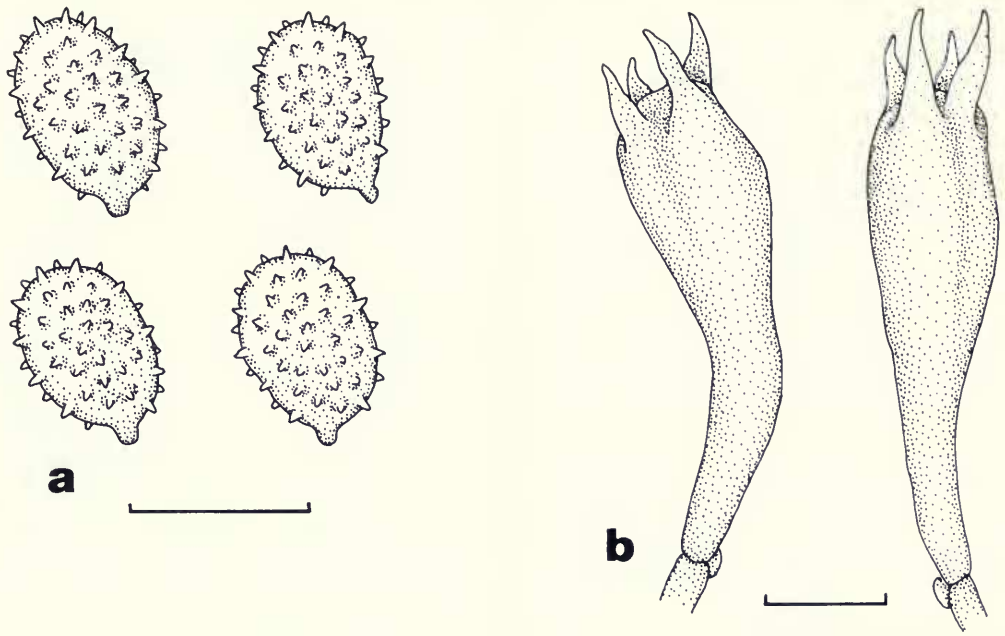


FIG. 8. Micromorphological features of *L. proxima* (GMM 2100): **a,** basidiospores; **b,** basidia. Scale line = 10 μm.

margin incurved to decurved, sometimes becoming plane, entire to undulate, occasionally becoming eroded with age; context thin, tapering quickly to margin, pinkish flesh color ("Japan Rose" to "Shell Pink"). **Lamellae** sinuate to adnate, occasionally arcuate, subdistant to distant, up to 10 mm broad, pinkish flesh color ("Flesh Color," "Pale Salmon Color"). **Stipe** (12–)24–72(–155) × 3–11 mm, equal to subclavate, often slightly bulbous, dry, fibrillose, often longitudinally striate, striations moderate to pronounced, most of stipe concolorous with pileus; base occasionally darker ("Rood's Brown"), striations concolorous with pileus or darker red ("Hay's Russet," "Pecan Brown,"or "Onion-skin Pink"). **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with scattered to numerous large fascicles of ± perpendicular hyphae; fascicles composed of 15–30 or more hyphae; terminal cells of fascicular hyphae 27.5–92 × 4.5–16(–30) μm, filamentous, subclavate, clavate, broadly clavate, capitate or ventricose-rostrate; walls up to 0.5 μm thick, light to moderate yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–19 μm diam., thin-walled, hyaline to light yellowish brown; cells filamentous to barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (23–)33–62 × 8–15 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. **Cheilocystidia** 19–66.5(–92) × 2–8.5 (–16.5) μm, filamentous to subclavate, occasionally subcapitate, often abundant, thin-walled hyaline. **Basidiospores** (excluding ornamentation) [265/20] 8–11(–12.5) × (6.5–)7–8.7(–9.2) μm ($\bar{x}$ = [8.7–]9–11.5 × 6.7–8[–8.8] μm), Q = (1.07–)1.16–1.49(–1.58) ($\bar{Q}$ = 1.24–1.34[–1.43]), broadly ellipsoid, ellipsoid or occasionally oblong, hyaline, echinulate; echinulae 0.5–1 μm long, occasionally with 1 or 2 long echinulae (up to 2 μm long) at apex, crowded; hilar appendix 1.3–2 μm long, prominent, truncate, plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2.5–17.5 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

SOMATIC CULTURE MAT MORPHOLOGY (N = 4; Appendix B)—**PDA: Radius** at week 3 = 3–17 mm, week 6 = 26–43 mm; **mat** felty, thick, tightly interwoven, not translucent, most of uniform thickness or with slightly thicker area near plug, in one (GMM 1525) forming concentric thicker-thinner bands, white to light tan; **margin** 1–2 mm broad, abruptly thinner or not well differentiated, silky to subfelty, thin, uneven, white; **plug** white

or becoming olive; **hyphae** morphologically undifferentiated. **MMN: Radius** at week 3 = (6–)16–32 mm, week 6 = (18–)43–64 mm; **mat** subfelty to felty, relatively thin to moderately thick, interwoven, translucent to not translucent, thicker near plug, uniform or thinner towards margin, white; **margin** abruptly thinner or not well differentiated, silky to subfelty, white; **plug** white; **hyphae** morphologically undifferentiated. **MEA: Radius** at week 3 = 11–26 mm, week 6 = 30–51 mm; **mat** subfelty to felty, thin to relatively thick, translucent, white; **margin** not well differentiated, somewhat thinner, white; **plug** white; **hyphae** morphologically undifferentiated, occasionally irregularly swollen.

HABITAT AND DISTRIBUTION—Scattered to gregarious; terrestrial, associated most commonly with Pinaceae, occasionally among mosses including *Sphagnum*; disturbed areas, early succession forests or under young planted pines in reforested areas. Cosmopolitan; common. Found throughout North America. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—*Laccaria proxima* can be distinguished from *L. laccata* by its more robust, more strongly colored basidiomata, nonstriate and slightly scaly to scaly pilei, and more elongate, finely echinulate basidiospores. *Laccaria proxima* is separated from *L. montana* in having smaller, more finely echinulate basidiospores and the more robust habit of its basidiomata. Collections of *L. proxima* can be differentiated from those of *L. oblongospora* by having less elongate, larger basidiospores, white basal mycelium, and culture mats that are white on MMN, PDA, and N6:5 media. A discussion of various interpretations of the name *L. proxima* is presented in the section on type specimens.

Mueller (1982, 1984, 1985) reported that cultures of some *L. proxima* were violet to purple on PDA and MMN media. On further analysis of the collections from which these violet culture mats were derived, it was determined that these specimens were *L. bicolor* and not *L. proxima*. The basidiospores observed from these collections were much smaller and had longer echinulae than those from other collections referable to *L. proxima*. The basidiospore dimensions and cultural characteristics fit my circumscription of *L. bicolor*.

Intra- and interspecific pairing studies have supported treatment of *L. proxima* as a discrete species. No isolate of *L. proxima* has been found to mate with any other putative taxa, and no intraspecific intersterility groups have been detected (Fries & Mueller, 1984; Mueller, unpubl. data). Further support for recognizing *L. proxima* as an autonomous species was obtained during analyses of mtDNA and rDNA RFLPs of select species of *Laccaria* (Gardes et al., 1990, 1991a). A low level of intraspecific heterogeneity in mtDNA and rDNA RFLPs was detected among three isolates of *L. proxima* used in these analyses, whereas their RFLPs were distinct from RFLPs of the other tested taxa.

Laccaria proxima has been reported from throughout North America. It has also commonly been collected in Europe (Clémençon, 1984; Contu, 1986; Mueller, 1991a). Watling (1987) reported that *L. proximella* Singer is the alpine equivalent of *L. proxima*. As discussed previously (Mueller, 1991a), I cannot support this contention based on the large number of collections referable to *L. proxima* that I have examined from alpine and boreal habitats in Europe and North America. My interpretation of *L. proximella* is that it differs from *L. proxima* by having violet strains (or mycelium?) at the stipe base and grows in very poor, rocky soil. I have collected material referable to *L. proximella* in southern Argentina and Chile.

Laccaria oblongospora G. M. Mueller. Figures 9–11, 53c,d, 67d.

Laccaria oblongospora G. M. Mueller, Mycotaxon 20: 108–112. 1984. TYPE: USA, Mississippi, Harrison Co.; DeSoto National Forest, Harrison Experimental Forest, Road H-8, 7 December 1980, *G. M. Mueller 1102* (TENN 42522) (TENN!, holotype).

MACROMORPHOLOGY—**Pileus** (5–)12–59 mm broad, obtuse to convex, becoming plane to uplifted, often depressed, not striate, finely fibrillose, becoming fibrillose-scaly, hygrophanous, brownish orange ("Vinaceous-Rufous," "Kaiser Brown," "Apricot Buff," "Burnt Sienna," or "Sanford's Brown"), occasionally vinaceous color ("Vinaceous-Brown," "Vinaceous-Russet" or "Japan Rose"); disc often darker, red-brown to dark orange-brown or occasionally vinaceous ("Dark Livid Brown," "Deep Brownish Vinaceous," "Hay's Russet," "Chocolate," "Vinaceous-Russet," or "Mahogany Red"); margin incurved to decurved, becoming plane to uplifted, entire to undulate, occasionally becoming eroded; context 1–2 mm thick, tapering quickly to margin, flesh color ("Pale Vinaceous-Pink"). **Lamellae** sinuate to adnate, oc-

casionally arcuate, subdistant to distant, broad, thick, pinkish flesh color ("Vinaceous-Pink," "Buff-Pink," "Light Congo Pink," or "Shell Pink"), occasionally vinaceous or violaceous ("Light Brownish Vinaceous," "Pale Brownish Vinaceous," or "Light Pinkish Lilac"). **Stipe** (11–)20–60(–65) × 2–12 mm, equal to subclavate, often slightly bulbous, dry, fibrillose, occasionally finely longitudinal-striate, concolorous with pileus; striations occasionally darker ("Pecan Brown"). **Basal mycelium** violet, soon fading to white. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of loosely interwoven hyphae with scattered large fascicles of ± perpendicular hyphae; fascicles composed of (5–)10–30 or more hyphae; terminal cells 32.5–71 × 7–24.5 μm, filamentous, subclavate, clavate, broadly clavate or capitate; walls up to 0.5 μm thick, light vinaceous; contents hyaline to light yellowish brown or light vinaceous. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, yellowish brown to light vinaceous toward pileipellis. **Lamellar trama** parallel; hyphae 3–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 24–35 × 6.5–10 μm, clavate, hyaline; sterigmata 4, up to 5.5 μm long. **Cheilocystidia** 31.5–53 × 3–7 μm, filamentous to subclavate, scattered, thin-walled, hyaline, found only in some collections. **Basidiospores** (excluding ornamentation) [75/5] 7.4–10 × 5–7 μm ($\bar{x}$ = 8.3–9.1 × 5.6–5.9 μm), Q = 1.3–1.76 ($\bar{Q}$ = 1.45–1.60), ellipsoid to oblong, occasionally subreniform, hyaline, echinulate; echinulae < 0.5(–1.4) μm long, those > 0.5 μm long restricted to basidiospore apex, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–11 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

SOMATIC CULTURE MAT MORPHOLOGY (N = 5; Appendix B)—**PDA: Radius** at week 3 = 28–39 mm, week 6 = 45–78 mm; **mat** felty, thick, tightly interwoven, with scattered small sectors of longer, loosely interwoven hyphae, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, not translucent, at first dark violet, soon fading, week 3 = light to moderate violet coloration restricted either to 2–3 mm band near margin or 4–5 mm zone near plug, most of mat light orange-brown, week 6 all light orange-brown, no violet coloration present; **margin** up to 5 mm broad, silky to subfelty, thin, uneven, light violet, becoming white; **plug** concolorous with mat; **hyphae** mostly morphologically undifferentiated, occasionally irregularly swollen, subcoralloid or coralloid. **MMN: Radius** at week 3 = most 48–56 mm, one isolate 30–36 mm, week 6 = most covering agar surface, one isolate 58–78 mm, **mat** subfelty to subwoolly, thin, becoming thicker, loosely interwoven, some with subwoolly to woolly or cottony narrow strands radiating out from the plug to margin, between strands thin, tightly appressed to agar surface, translucent, becoming somewhat translucent, at first light violet, soon fading to light violet or white, **margin** not well differentiated, thin, uneven, concolorous; **plug** concolorous; **hyphae** most morphologically undifferentiated, occasionally irregularly swollen, subcoralloid or coralloid. **MEA: Radius** at week 3 = 26–40 mm, week 6 = 51–78 mm; **mat** subfelty, thin, loosely interwoven, some with 1–3 narrow, slightly thicker concentric bands, tightly appressed to agar surface, translucent, white; **margin** 1–2 mm broad, not well differentiated, even to uneven, white; **plug** white; **hyphae** morphologically undifferentiated, occasionally irregularly swollen or subcoralloid.

HABITAT AND DISTRIBUTION—Gregarious; in very sandy soil under *Pinus palustris* Miller; Gulf Coast. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—*Laccaria oblongospora* often appears similar to *L. proxima* or *L. trichodermophora* in the field. It differs from *L. proxima* in basidiospore shape and size, basal mycelium color, and cultural features. It can be distinguished from *L. trichodermophora* primarily on basidiospore shape and echinulae length.

Much variation in basidioma color was observed in this taxon. Most specimens exhibited the typical orange-brown coloration of *L. laccata sensu lato.* Scattered among these were a few individual fruitbodies which were vinaceous to violaceous in color (e.g., TENN 42524). Initially, these vinaceous collections were thought to represent a separate taxon. However, because of the occurrence of intermediate color forms (orange-brown pilei and stipes with violaceous lamellae) and identical culture mat morphologies, they have been treated as contaxic.

Intercollection pairing studies support the treatment of *L. oblongospora* as a separate species. Isolates from the two stocks obtained during this study were intercompatible with each other but intersterile with all tested isolates of other species, including isolates of *L. proxima.* Material of *L. ob-*

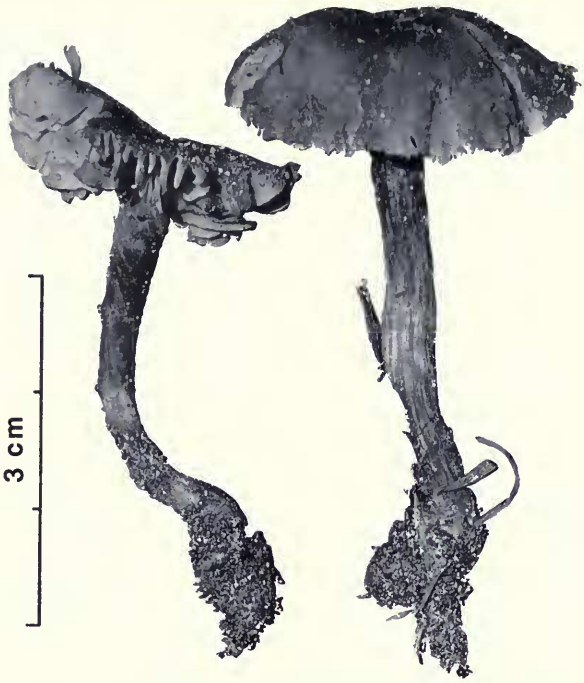


FIG. 9. Basidiomata of *L. oblongospora* (GMM 2310).

FIG. 10. Somatic culture mats of *L. oblongospora* (GMM 1105). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.

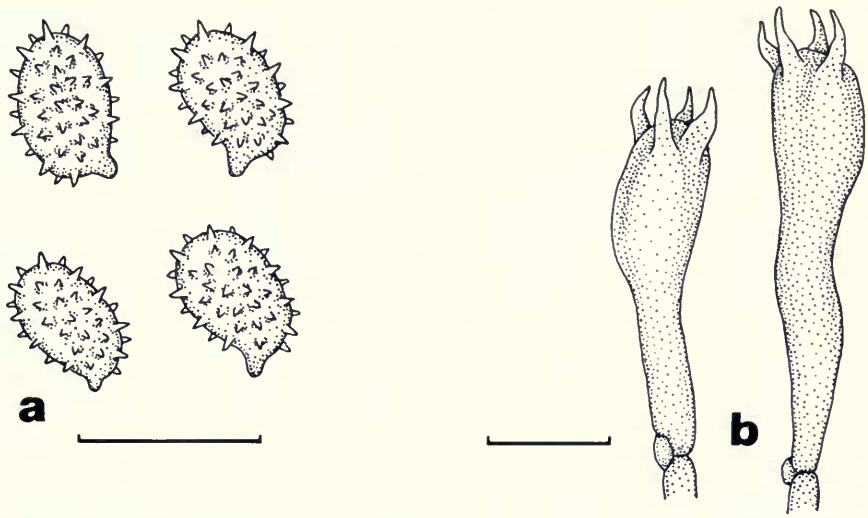


FIG. 11. Micromorphological features of *L. oblongospora* (GMM 2310): **a**, basidiospores; **b**, basidia. Scale line = 10 μm.

longospora was not included in the analyses of mtDNA or rDNA RFLPs.

Laccaria oblongospora was consistently placed in *Laccaria* metasection *Laccaria* during cladistic analyses. Phylogenetic relationships between the taxa in this metasection, however, were not resolved during these analyses. If this is the correct placement of *L. oblongospora,* the pigment(s) responsible for the violet mycelium at stipe bases and culture mats would be plesiomorphic and would not be informative for resolving relationships within the genus (see Phylogenetic Considerations for further discussion).

Only a few populations of this species have been located. All of them were either in eastern Texas or southern Mississippi. Several of these populations were very large and consisted of numerous basidiomata. Specimens of *L. oblongospora* have only been encountered near stands of *Pinus palustris.*

Laccaria laccata (Scopoli: Fries) Cooke.[2]

≡ *Agaricus laccatus* Scopoli, Flora Carniolica 2: 444. 1772. TYPE: Sweden, Femsjö, 17 August 1964, *Singer 4083* (BAFC!; neotype *fide* Singer, 1967).

≡ *Agaricus laccatus* Scopoli: Fries, Systema Mycologica 1: 106. 1821.

≡ *Clitocybe laccata* (Scopoli: Fries) Kummer, Führer in die Pilzkunde: 122. 1871.

≡ *Camarophyllus laccatus* (Scopoli: Fries) P. Karst., Ryssl., Finl. Skand. Halföns Hattsvamp.: 231. 1879.

≡ *Laccaria laccata* (Scopoli: Fries) Cooke, Grevillea 12: 70. 1884.

≡ *Omphalia laccata* (Scopoli: Fries) Quélet, Enchiridion Fungorum: 2C. 1886.

≡ *Collybia laccata* (Scopoli: Fries) Quélet, Flore Mycologique: 237. 1888.

≡ *Russuliopsis laccata* (Scopoli: Fries) Schroeter *in* Cohn, Krypt.-Fl. Schlesien 3: 622. 1889.

= *Agaricus carneus* Schaeffer, Fungorum Bavaria 4: 71, fig. 304. 1774. TYPE: Lacking.

= *Agaricus farinaceus* Hudson, Flora Anglica: 616. 1778. TYPE: Lacking.

≡ *Omphalia farinacea* (Hudson) S. F. Gray, Nat. Arr. Brit. Pl. 1: 612. 1821.

≡ *Laccaria farinacea* (Hudson) Singer *in* Singer & Moser, Mycopathol. Mycol. Appl. 26: 149. 1965. [not validly published, basionym lacking].

≡ *Laccaria farinacea* (Hudson) Singer, Sydowia Beih. 7: 8. 1973.

= *Agaricus rosellus* Batch, Elench. fung. Continuatio prima: 121, fig. 99. 1786; *non Agaricus rosellus* Fries: Fries, Systema Mycologica 1: 151. 1821. [= *Mycena rosella*].

≡ *Omphalia rosella* S. F. Gray, Nat. Arr. Brit. Pl. 1: 613. 1821.

≡ *Russuliopsis laccata* var. *rosellus* (S. F. Gray) Schroeter *in* Cohn, Krypt.-Fl. Schlesien 3: 623. 1889.

≡ *Laccaria laccata* var. *rosella* (S. F. Gray) Singer, Ann. Mycol. 41: 17. 1943.

= *Agaricus subcarneus* Batch, Elench. fung. Continuatio prima.: 121, fig. 100. 1786.

[2] Berkeley and Broome (1883) did not make any new combinations when proposing the genus *Laccaria.* Consequently, they did not validly publish *L. laccata* (Greuter et al., 1988, Art. 33.1).

= *Agaricus* (*Clitocybe*) *glaucipes* Berkeley & Curtis, Ann. Mag. Nat. Hist., III. 4: 284. 1859.

Excluded—*Laccaria farinacea* (Hudson) Singer, Sydowia Beih. 7: 8. 1973. [= *L. trichodermophora* G. M. Mueller].

As discussed in Mueller and Vellinga (1986), Singer's typification of *L. laccata* (Singer, 1967) has perpetuated confusion in the delimitation of *L. laccata.* The specimen that he chose is not representative of the species because the micromorphological characters of the collection are near the extreme range for the taxon. To date, very few collections referable to *L. laccata* have been encountered that have basidiospores as elongated as the neotype (Mueller & Vellinga, 1986; Mueller, 1991a).

Singer (1946, 1967, 1973, 1977), Bon (1983), and others have proposed a number of species and subspecific taxa in an attempt to delimit natural taxa within this highly variable group. Descriptions of the type specimens of most of these names are presented later in this monograph (see Type Studies). Type specimens of the majority of these names have basidiospores that are globose to subglobose in shape. Only collections from the type variety and three other varieties were found to have ellipsoid basidiospores ($\bar{Q}$ = 1.25–1.3) (see Type Studies and Mueller & Vellinga, 1986). For these reasons, Mueller and Vellinga (1986) and Mueller (1991a) treated most of the proposed varieties of *L. laccata, L. tetraspora,* and *L. affinis* (Singer) Bon as synonyms of one of three varieties: *L. laccata* var. *laccata, L. laccata* var. *moelleri,* and *L. laccata* var. *pallidifolia.*

Additional morphometric and intercollection pairing studies were undertaken, and these data were compared with information on mtDNA and rDNA RFLPs (Gardes et al., 1990, 1991a) in an attempt to resolve systematic problems surrounding *L. laccata sensu lato* (Mueller, 1991c). Based on a synthesis of these data, I recognize the following taxa in this complex: *L. laccata* var. *laccata, L. laccata* var. *moelleri, L. laccata* var. *pallidifolia, L. longipes, L. ohiensis* (= *L. tetraspora*), and *L. striatula.* All of these except *L. laccata* var. *moelleri* occur in North America and will be treated in detail below. *Laccaria laccata* var. *moelleri* is discussed with *L. longipes* below.

Laccaria laccata var. **laccata.** Figure 64d.

= *Agaricus* (*Clitocybe*) *laccatus* var. *lutea* Fries, Epicr. syst. mycol.: 79. 1836–1838.

= *Agaricus* (*Clitocybe*) *laccatus* var. [*pileo*] *luteoviolaceo* Fries, Epicr. syst. mycol.: 79. 1836–1838.

= *Agaricus* (*Clitocybe*) *laccatus* var. [*obscure*] *violacea* Fries, Epicr. syst. mycol.: 79. 1836–1838.

= *Agaricus* (*Clitocybe*) *laccatus* var. *rufocarnea* Fries, Epicr. syst. mycol.: 79. 1836–1838.

= *Laccaria laccata* var. *carbonicola* Singer, Bull. Soc. Mycol. France 83: 110. 1967.

= *Laccaria laccata* var. *gibba* Singer, Beih. Nova Hedwigia 29: 27. 1969.

= *Laccaria laccata* var. *vulcanica* Singer *ex* Veselsky & Singer, Pl. Syst. Evol. 126: 362. 1977.

= *Russuliopsis laccata* var. *rosellus* f. *pusilla* Schroeter *in* Cohn, Krypt.-Fl. Schlesien: 623. 1889.

MACROMORPHOLOGY (*Teste* Singer, 1967)—**Pileus** (6–)10–45 mm broad, convex becoming plane, often slightly depressed, occasionally umbonate, slightly striate, glabrous to finely fibrillose, occasionally becoming fibrillose-scaly, hygrophanous, reddish brown becoming pale ochre when dry. **Lamellae** adnate to adnate-subdecurrent, distant, broad, rather pale and dull reddish color. **Stipe** 40–60(–90) × 2–7(–14) mm, equal to slightly clavate, fibrous with innate fibrils, concolorous with pileus or concolorous with lamellae at apex and brown toward base. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae 38–80 × 6.5–18 μm, filamentous, slightly swollen, subclavate or capitate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel, hyphae 2.5–12 μm diam., thin-walled, hyaline; cells barrel-shaped. **Subhymenium** undifferentiated. **Basidia** 27.5–48 × 7–16.5 μm, clavate, hyaline; sterigmata 4, up to 12 μm long. **Pleurocystidia** lacking. **Cheilocystidia** 25–70 × 2–7.5 μm, filamentous, absent to common, hyaline. **Basidiospores** (excluding ornamentation) [210/7] (7–)7.7–9.7(–11) × (5–)6.4–8(–8.5) μm ($\bar{x}$ = 7.8–9.2 × 6.3–7.1 μm), Q = (1.08–)1.18–1.35(–1.46) ($\bar{Q}$ = 1.2–1.3), subglobose to ellipsoid, hyaline, echinulate; echinulae 1–1.8(–2.3) μm long, ≤ 1 μm wide at base; hilar appendix up to 1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate.

HABITAT AND DISTRIBUTION—Solitary to gregarious; terrestrial, host unknown. Reported from only a few localities in Europe and North America; not abundant. Not commonly collected. A list of collections examined is provided in Appendix A.

OBSERVATIONS—The type variety is distinguished from other varieties of *L. laccata* by having broadly ellipsoid to ellipsoid, moderately ornamented basidiospores. It is sometimes difficult to differentiate *L. laccata* var. *laccata* from *L. proxima* without information on macromorphology. Major differences between them are the more robust, darker colored, scaly basidiomata of *L. proxima,* and the more coarsely ornamented basidiospores of *L. laccata* var. *laccata.*

The description presented above was based on a compilation of the protologues of the type collections for the names treated as synonyms of *L. laccata* var. *laccata* plus several collections referable to this taxon found in Swedish herbaria. I have not collected specimens referable to this taxon.

No isolates of specimens referable to *L. laccata* var. *laccata* have been included in the intra- and interspecific pairing studies (Fries & Mueller, 1984; Mueller, 1991c) or in the analyses of mtDNA and rDNA RFLPs (Gardes et al., 1990, 1991a), because I have not obtained cultures of this taxon. Data on the results of pairing studies using other recognized varieties are discussed below.

Based on available herbarium specimens, *L. laccata* var. *laccata* is not common, as few collections were encountered among the borrowed material. In Sweden this taxon appears to have a very restricted distribution. Five of the six Swedish collections examined came from Femsjö and may be from the same population or even the same individual mycelium (Mueller, 1991a). This is the same general locality from where Singer (1967) obtained the type specimen.

Laccaria laccata var. **pallidifolia** (Peck) Peck. Figures 12–14, 54d–f, 68c.

≡ *Clitocybe laccata* var. *pallidifolia* Peck, Annual Rep. New York State Bot. 43: 274. 1890. TYPE: USA, New York, Selkirk, October, *C. H. Peck s.n.* (NYS!, holotype).
≡ *Laccaria laccata* var. *pallidifolia* (Peck) Peck, Annual Rep. New York State Bot. 157: 92. 1912.
= *Laccaria laccata* var. *decurrens* Peck, Annual Rep. New York State Bot. 157: 92. 1912.
= *Laccaria laccata* f. *minuta* Imai, J. Fac. Sci. Hokkaido Imp. Univ., Ser. 5, Bot. 18: 90. 1938.
≡ *Laccaria laccata* var. *minuta* (Imai) Hongo, Mem. Shig. Univ. 9: 58. 1959.
= *Laccaria laccata* var. *anglica* Singer, Bull. Soc. Mycol. France 83: 110–111. 1967.
≡ *Laccaria anglica* (Singer) Bon, Doc. Mycol. 11: 22. 1981 [not validly published, basionym lacking].
≡ *Laccaria affinis* var. *anglica* (Singer) Bon, Doc. Mycol. 13: 50. 1983.
= *Laccaria laccata* var. *affinis* Singer, Bull. Soc. Mycol. France 83: 111. 1967.
≡ *Laccaria affinis* (Singer) Bon, Doc. Mycol. 13: 49. 1983.
= *Laccaria laccata* var. *chilensis* Singer, Bull. Soc. Mycol. France 83: 109. 1967.
= *Laccaria laccata* var. *subalpina* Singer, Pl. Syst. Evol. 126: 365. 1977.
= *Laccaria tetraspora* var. *peladae* Singer, Bull. Soc. Mycol. France 83: 117. 1967.
≡ *Laccaria laccata* var. *peladae* (Singer) Singer, Pl. Syst. Evol. 126: 366. 1977.
= *Laccaria laccata* var. *tatrensis* Singer, Pl. Syst. Evol. 126: 367. 1977.
= *Laccaria laccata* var. *intermedia* Singer, Pl. Syst. Evol. 126: 368. 1977.

MACROMORPHOLOGY—**Pileus** 10–45(–60) mm broad, obtuse to convex, often becoming plane to uplifted, often depressed, striate to not striate, occasionally strongly striate to plicate-striate, sometimes translucent-striate when fresh, finely fibrillose to fibrillose-scaly, infrequently slightly scaly, hygrophanous, orange-brown when fresh, becoming buff color ("Sanford's Brown," "Orange Rufous," "Hazel," "Cinnamon-Rufous," "Pinkish Cinnamon," or "Light Vinaceous-Cinnamon"), fading lighter ("Apricot Buff," "Salmon Color," "Light Pinkish Cinnamon," or "Pinkish Buff"), finally to buff ("Pale Ochraceous Buff"); disc occasionally darker orange-brown or red-brown ("Hay's Russet," "Ochraceous Tawny" or "Buckthorn Brown"); margin incurved to decurved, becoming plane to uplifted, entire to undulate, occasionally becoming eroded in age; context thin, tapering quickly to margin, concolorous. **Lamellae** sinuate, adnate or arcuate, rarely decurrent, close to distant, narrow to broad, relatively thin to thick, pinkish flesh color ("Flesh Color," "Salmon-Buff," "Pale Salmon Color," "Flesh-Pink," or "Light Vinaceous-Cinnamon"), some becoming slightly vinaceous with age (near "Light Grayish-Vinaceous"). **Stipe** (12–)20–65(–106) × 2–4(–8) mm, equal, subclavate or tapering toward base, occasionally slightly bulbous, dry, fibrillose, not striate to finely longitudinally striate, rarely with pronounced striations, concolorous with stipe; context stuffed, becoming hollow, concolorous with pileus context. **Basal mycelium** sparse to copious, always white. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–15 (–30) hyphae; terminal cells of fascicular hyphae 6–101 × 3–37.5 μm, filamentous, subclavate, cla-

FIG. 12. Basidiomata of *L. laccata* var. *pallidifolia* (GMM 1735).

FIG. 13. Somatic culture mats of *L. laccata* var. *pallidifolia* (GMM 1011). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.

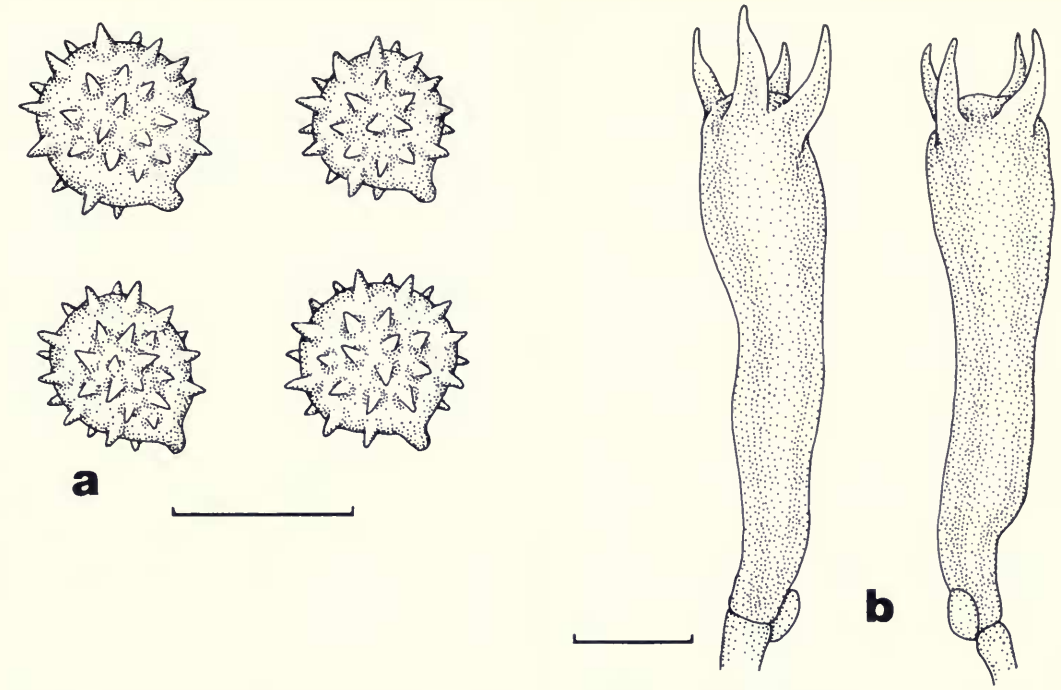


FIG. 14. Micromorphological features of *L. laccata* var. *pallidifolia* (GMM 1845): **a**, basidiospores; **b**, basidia. Scale line = 10 μm.

vate, subcapitate or ventricose-rostrate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 2–17.5 μm diam., thin-walled, hyaline to light yellowish brown; cells filamentous to barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 27.5–55 × 7.5–13.5(–16.5) μm, clavate, hyaline; sterigmata 4, up to 7 μm long. **Cheilocystidia** 23–55 × 2–7.5 μm, filamentous to subclavate, occasionally strangulate, absent or scattered to abundant, thin-walled, hyaline. **Basidiospores** (excluding ornamentation) [1,000/65] (6.4–)7.4–10(–13) × (6–)7–10(–11.5) μm ($\bar{x}$ = [7.3–]8.2–9[–9.6] × [6.7–]7.6–8.6 μm), Q = 1–1.13(–1.3) ($\bar{Q}$ = 1–1.5[–1.2]), globose to subglobose, occasionally broadly ellipsoid, hyaline, echinulate; echinulae (0.5–)1–2 μm long, ≤ 1 μm wide at base, relatively scarce to crowded; hilar appendix 1.3–2.2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate or biguttulate. **Basal mycelium hyphae** mostly 3–10.5 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

SOMATIC CULTURE MAT MORPHOLOGY (N = 11; Appendix B)—**PDA: Radius** at week 3 = 7–23 mm or 62–73 mm, week 6 = 18–27 or 90 mm (agar surface covered); **mat** felty, thick, tightly interwoven, some appearing almost crustose, tightly appressed to agar surface, occasionally forming cottony to felty aerial layer away from plug, not translucent, white, in some becoming dark olive brown or light chocolate color away from plug; **margin** narrow to moderately broad, silky to subfelty, thin, white, entire to undulate; **plug** occasionally covered with cottony white hyphae or with long serial aggregations of hyphae growing away from top of plug, white, often becoming dark olive brown or light chocolate color; **hyphae** morphologically undifferentiated, rarely irregularly swollen. **MMN: Radius** at week 3 = 13–19 mm or (25–)29–52 mm, week 6 = 26–45 mm or 75 mm to covering agar surface; **mat** subfelty, felty or silky, moderately thick, interwoven, in one isolate (TENN 42964) with several radially arranged pie-shaped thicker sectors, tightly appressed to agar surface, translucent, white; **margin** narrow, silky to subfelty, not well differentiated, even to undulate, occasionally somewhat serrate, white; **plug** white; **hyphae** morphologically undifferentiated,

occasionally coralloid. **MEA: Radius** at week 3 = 12–33 mm or 53–62 mm, week 6 = 23–54 mm or covering agar surface; **mat** silky to subfelty, thin to moderate, appearing combed to loosely interwoven, occasionally becoming thicker near plug, tightly appressed to agar surface, translucent, white; **margin** not well differentiated, thin, entire to slightly serrate, white; **plug** white; **hyphae** morphologically undifferentiated.

HABITAT AND DISTRIBUTION—Solitary to gregarious, occasionally caespitose, associated with Pinaceae, Fagaceae, and Betulaceae; cosmopolitan; abundant. Collected throughout North America. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—*Laccaria laccata* var. *pallidifolia* is characterized by having small- to moderate-sized, orange-brown, glabrous to finely scaly basidiomata, and basidia that bear four globose to subglobose, moderately echinulate basidiospores.

Mueller and Vellinga (1986) and Mueller (1991a) included collections now treated as *L. ohiensis* (= *L. tetraspora*) within the concept of this taxon. Reasons for this given by Mueller and Vellinga (1986) included: (1) the macro- and micromorphology of several of the proposed varieties intergraded between the two putative species; (2) basidioma and basidiospore size, as well as basidiospore ornamentation length, appeared to form a continuum for collections in this group; and (3) somatic culture mat morphology did not appear to vary between isolates referable to either of these taxa. It was not possible for Fries and Mueller (1984) to distinguish between collections of the two intersterility groups (mating groups III and IV) that they detected in the tested Swedish material of *L. laccata* on the basis of basidioma and basidiospore size and basidiospore ornamentation length.

Several additional intersterility groups have since been detected in North America (Mueller, 1991c). Each of these groups was found to differ markedly in RFLPs of mtDNA and rDNA (Gardes et al., 1990, 1991a). Subsequent morphometric analyses have shown that collections of some of these intersterility groups, but not others, were segregated during morphometric analyses of basidiospore data (Mueller, 1991c). Two groups were clearly delimited during morphometric analyses: one group consisted of collections with globose basidiospores with echinulae > 1.5 μm long and > 1.2 μm wide at the base; the other group consisted of specimens with globose to subglobose basidiospores with echinulae 0.7–2 μm long and ≤ 1 μm wide at the base (Mueller, 1991c). The first group consisted of collections referable to *L. ohiensis* and *L. striatula*; collections in the second group are referable to either *L. laccata* var. *pallidifolia, L. laccata* var. *moelleri,* or *L. longipes.*

Laccaria laccata var. *pallidifolia* is differentiated from *L. ohiensis* primarily by having narrow basidiospore echinulae. Collections of *L. laccata* var. *pallidifolia* with small basidiomata and globose basidiospores (characteristics of *L. ohiensis*) are occasionally encountered.

Laccaria laccata var. *pallidifolia* is differentiated from *L. striatula* on the basis of differences in basidiospore ornamentation and macromorphological features. Collections of *L. striatula* have relatively long, glabrous stipes that are usually darker than the strongly striate pileus.

Laccaria laccata var. *pallidifolia* is differentiated from *L. longipes* by having shorter stipes and larger basidiospores.

Laccaria laccata var. *pallidifolia* is the most commonly encountered taxon in the complex and can be found throughout the United States and Canada. No apparent habitat preference could be determined from the material collected during this study.

Laccaria longipes G. M. Mueller. Figures 15, 16, 54a, 65c.

Laccaria longipes G. M. Mueller, Mycotaxon 40: 145–150. 1991. TYPE: Canada, Ontario, Nipissing District, Algonquin Provincial Park, Spruce Bog Trail, among *Sphagnum* under *Picea mariana, Larix laricina,* and *Alnus rugosa,* 18 September 1984, *G. M. Mueller 1929* (F!, holotype).

MACROMORPHOLOGY—**Pileus** 11–55(–78) mm broad, convex to broadly convex, often becoming plane to uplifted, often centrally depressed, slightly to moderately translucent-striate, finely fibrillose, orange-brown (6B5–6D7) fading to buff in age; margin incurved to decurved or plane, entire to undulate, becoming slightly eroded. **Lamellae** adnate, distant, thick, up to 10 mm broad, light flesh color (near 6A2). **Stipe** 67–138(–165) × 3–9 mm, equal with slightly swollen base or narrowly clavate, dry, slightly to moderately fibrillose-striate, concolorous with pileus. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of radially arranged barrel-shaped hyphae with occasional scattered small fascicles of 10–30 ± perpendicular hyphae; terminal cells 5–10 μm, morphologically

undifferentiated to subclavate, hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline to light yellowish brown. **Lamellar trama** of parallel to subparallel hyphae, mostly 3–19 μm diam., thin-walled, hyaline; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 28–44 × 7–10 μm, clavate, hyaline; sterigmata 4, up to 10 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) [158/7] 7–8.5(–9) × 6–7.8(–8.4) μm ($\bar{x}$ = 7.6–7.8 × 6.8–7.2 μm), Q = (1–)1.05–1.2(–1.3) ($\bar{Q}$ = 1.08–1.13), subglobose to broadly ellipsoid, occasionally globose or ellipsoid, hyaline, echinulate; echinulae (0.7–)1–1.5(–2) μm long, less than 1 μm wide at base.

Somatic Culture Mat Morphology (N = 1; GMM 1929)—**PDA: Radius** at week 6 = 43 mm; **mat** felty, thick, tightly interwoven, tightly appressed to agar surface, not translucent, uniform texture near plug, forming dendritic thicker strands from midpoint to margin, tan to olive brown; **margin** ≤ 6 mm broad, subfelty to silky, abruptly thinner than mat, tan; **hyphae** 2.5–5 μm diam., morphologically undifferentiated. **MMN: Radius** at week 6 = 28 mm; **mat** felty, thick, tightly interwoven, tightly appressed to agar surface, uniform texture, dull white; **margin** up to 5 mm broad, irregular, white; **hyphae** 2.5–8 μm diam., morphologically undifferentiated, occasionally irregularly swollen. **MEA: Radius** at week 6 = 42 mm; **mat** subfelty, thin, translucent, white; **margin** 2–3 mm broad, not well differentiated, white; **hyphae** 2.5–8 μm diam., most morphologically undifferentiated, occasionally irregularly swollen.

Habitat and Distribution—Among mosses, especially *Sphagnum,* usually under *Picea mariana* (Mill.) B.S.P., *Larix laricina* (Du Roi) K. Koch, and *Alnus rugosa* (Du Roi) Spreng. Reported to date from the Great Lakes region (southern Ontario, Michigan, Wisconsin, Minnesota) and New York. A list of specimens examined is presented in Appendix A.

Observations—*Laccaria longipes* can be distinguished from other members of the *L. laccata* complex by its relatively small, subglobose basidiospores, long stipe, and restricted habitat. *Laccaria laccata* var. *moelleri* also occurs in bogs and has similar macromorphological features but differs in having larger basidiospores ($\bar{x}$ = 8–10 × 7.3–8.3 μm). *Laccaria galerinoides* Singer is another taxon that grows among *Sphagnum.* It appears to be restricted to southern Argentina and Chile and has only been reported from under *Nothofagus antarctica* (G. Forster) Derst. *Laccaria galerinoides* differs from the two Northern Hemispheric taxa in having smaller, darker colored basidiomata and more elongate basidiospores ($\bar{Q}$ = 1.34; holotype).

Tested isolates of *L. longipes* were intersterile with all other tested isolates of the *L. laccata* complex, including isolates of *L. laccata* var. *moelleri* (Mueller, 1991b,c). RFLPs of mtDNA and rDNA indicate that divergence has occurred between *L. longipes* and other taxa in the *L. laccata* complex (Gardes et al., 1990, 1991a). Although isolates of *L. laccata* var. *moelleri* were intersterile with all tested North American isolates, including *L. laccata* var. *pallidifolia* (intersterility group 1), they were intercompatible with the tested Swedish isolates of *L. laccata* var. *pallidifolia,* and both taxa belong to intersterility group 3 (Mueller & Vellinga, 1986; Mueller, 1991b,c). Data on potential molecular divergence between these morphologically distinct taxa do not yet exist, however, because both isolates of intersterility group 3 tested by Gardes et al. (1990, 1991a) are referable to *L. laccata* var. *moelleri.*

Collections of *L. longipes* were cited as *L. laccata* var. *moelleri* in several recent publications (Doudrick & Anderson, 1989; Gardes et al., 1990, 1991a). The decision to treat the North American and Swedish populations as distinct taxa occurred only after a synthesis of the data on RFLPs with data on intercollection pairing reactions and morphometric similarities (Mueller, 1991b,c).

It is not yet clear whether *L. longipes* and *L. laccata* var. *moelleri* are closely related or if their similar macromorphology is due to convergence resulting from their occurrence among *Sphagnum* and other mosses.

Laccaria fraterna (Cooke & Massee: Saccardo) Pegler. Figures 17, 18, 54b, 62d.

≡ *Agaricus fraternus* Cooke & Massee *in* Cooke, Grevillea 16: 31. 1887, *non Agaricus fraternus* Lasch, Linnaea 3: 402. 1828. [= *Cortinarius* sp.]. TYPE: Australia: vic. Port Phillip, *French no. 1* (K!, holotype).

≡ *Naucoria fraterna* (Cooke & Massee) Saccardo, Syll. Fung. 9: 110. 1891.

≡ *Laccaria fraterna* (Cooke & Massee: Saccardo) Pegler, Austral. J. Bot. 13: 332. 1956.

= *Naucoria goosensiae* Beeli, Bull. Soc. Roy. Bot. Belgique 61: 88. 1928.

≡ *Laccaria laccata* f. *bispora* Heinemann, Bull. Jard. Bot. État 34: 310. 1964. [change of name].

= *Laccaria lateritia* Malençon, Bull. Soc. Mycol. France 82: 189. 1966.

FIG. 15. Basidiomata of *L. longipes* (GMM 1929).

MACROMORPHOLOGY—**Pileus** 9–35(–55) mm broad, strongly convex to convex, becoming plane to uplifted, often slightly depressed, not striate to slightly translucent-striate, finely fibrillose to fibrillose, rusty red-brown (8D7–9E7), eventually becoming buff; margin decurved to plane, entire to slightly undulate; contex thin, concolorous with pileus. **Lamellae** adnate, moderately distant to distant, thick, pinkish rose (near 8A3). **Stipe** (17–)25–65 × 3–5 mm, equal or slightly clavate, at times caespitose, dry, fibrillose, moderately longitudinally striate, concolorous or slightly darker than

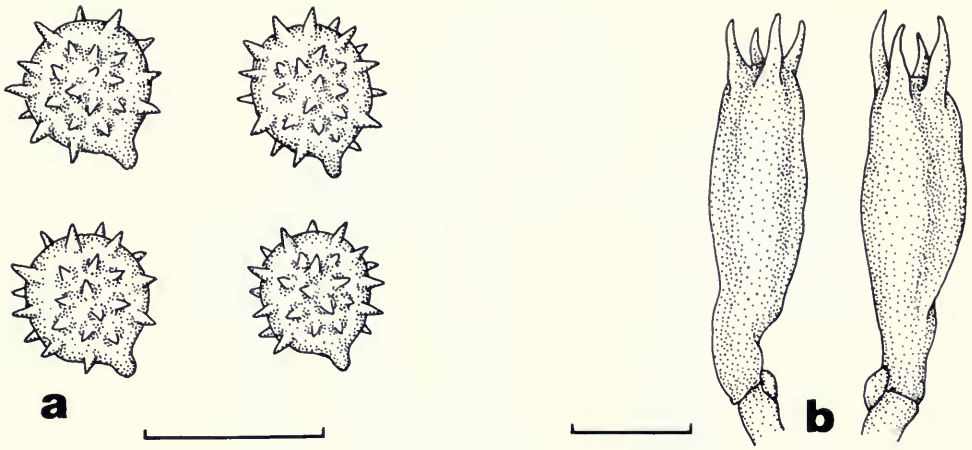


FIG. 16. Micromorphological features of *L. longipes* (GMM 1929): **a**, basidiospores; **b**, basidia. Scale line = 10 μm.

pileus (9C5–9D6). **Basal mycelium** white, often copious. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae 26–69 × 6.5–15 μm, filamentous to clavate; walls up to 0.5 μm thick, light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–10(–15.5) μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 29–46 × 8–12 μm, clavate, hyaline; sterigmata 2(3), up to 11 μm long. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) [100/4] (7.8–) 8.5–11(–13.5) × (7.4–)8–10.5(–13.5) μm ($\bar{x}$ = 9.7–10.5 × 8.9–9.9 μm), Q = 1–1.18(–1.22) ($\bar{Q}$ = 1.01–1.11), globose to subglobose, hyaline, strongly echinulate; echinulae 1–1.8 μm long, ≤ 1 μm wide at base, crowded; hilar appendix 1.3–2.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate.

HABITAT AND DISTRIBUTION—Under *Eucalyptus* and other introduced trees. *Laccaria fraterna* was probably introduced along with *Eucalyptus* throughout the world. Commonly collected under *Eucalyptus* throughout the world, including North America. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—*Laccaria fraterna* can be distinguished from other small *Laccaria* taxa by its rusty red-brown basidiomata and 2-sterigmate basidia that bear globose to broadly ellipsoid basidiospores that are < 11 μm long.

There has been considerable confusion in the literature concerning the correct name for this taxon. Some workers have used the name *L. ohiensis* for this taxon (e.g., Singer, 1942, 1946, 1949, 1967, 1975, 1977; McNabb, 1972), but an examination of the holotype revealed that *L. ohiensis* has 4-sterigmate basidia (see Type Descriptions). Although the most commonly used name for the taxon has been *L. lateritia,* the correct name for this taxon is *L. fraterna* (Mueller & Vellinga, 1986; Vellinga & Mueller, 1987).

Tom W. May (University of Melbourne, pers. comm.) reports the finding of a potentially paratypic collection at MEL that better fits the protologue but that is not contaxic with the type specimen housed at K. It has been assumed that the report of ellipsoid basidiospores in the original diagnosis of *A. fraternus* probably referred to another collection on the type sheet at K that was collected in New Zealand (Pegler, 1965; Mueller & Vellinga, 1986). If the collection housed at MEL is lectotypified, *A. fraternus* would not fit into the generic circumscription of *Laccaria* and the correct basionym for the taxon treated here would be *N. goosensiae.*

Ballero and Contu (1989) described *L. singeri* Ballero & Contu. This name, however, is a later homonym of *L. singeri* Locquin & Sarwal (Sarwal & Locquin, 1983) and Mueller and Vellinga (1990) renamed it *L. impolita* Vellinga & G. M. Mueller. *Laccaria impolita* is similar in micromorphology to *L. fraterna* but differs from it in basidioma

FIG. 17. Basidiomata of *L. fraterna* (GMM 2126).

color, lack of pileus striations, and ectomycorrhizal hosts (north temperate trees). See the discussion under *L. impolita* in Type Studies.

Laccaria montana Singer. Figures 19, 20, 54c, 66d.

≡ *Laccaria montana* Singer, Sydowia 7: 89. 1973. TYPE: Switzerland, Valais, prope flumen Borgne de Ferpecle, 1955–1960 m alt., 11 July 1971, *Singer M5464* (F!, holotype).

= *Laccaria laccata* var. *montana* Möller, Fungi of the Faeröes: 269. 1945.

= *Russuliopsis laccata* var. *rosella* f. *pusilla* Larsen, Bot. Iceland, vol. II, part IV 9: 525. 1932.

≡ *Laccaria laccata* var. *pusilla* (Larsen) Singer, Bull. Soc. Mycol. France 83: 109. 1967. [*non L. laccata* f. *pusilla* Schroeter *in* Cohn, Krypt.-Fl. Schlesien 3: 623. 1889 (= *L. laccata*)].

MACROMORPHOLOGY—**Pileus** 6–35 mm broad, convex to plane, becoming uplifted, often depressed, occasionally umbonate when young, usually plicate-striate when fresh, fibrillose to finely fibrillose-scaly, hygrophanous, brownish orange ("Hazel" to "Cinnamon-Rufous"), fading to buff color; margin decurved to plane, entire to undulate, occasionally becoming eroded; context ≤ 1 mm thick at disc, flesh color "Buff-Pink"). **Lamellae** sinuate to decurrent, close to distant, pinkish flesh color to light vinaceous ("Vinaceous-Pink"). **Stipe** 13–54(–101) × 2–4(–7) mm, equal or tapering slightly toward base or apex, occasionally swollen at base, occasionally caespitose, dry, fibrillose, not striate to moderately longitudinally striate, concolorous with pileus. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–30 hyphae; terminal cells of fascicular hyphae 39–51 × 5.5–10 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel, hyphae mostly 2.5–20 μm diam., thin-walled, hyaline to light yellowish brown; cells filamentous to barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 34.5–55 × 10–15.5 μm, clavate, hyaline; sterigmata 4, up to 11 μm long. **Cheilocystidia** 32–55.5 × 3–4.5(–7.5) μm, filamentous to subclavate,

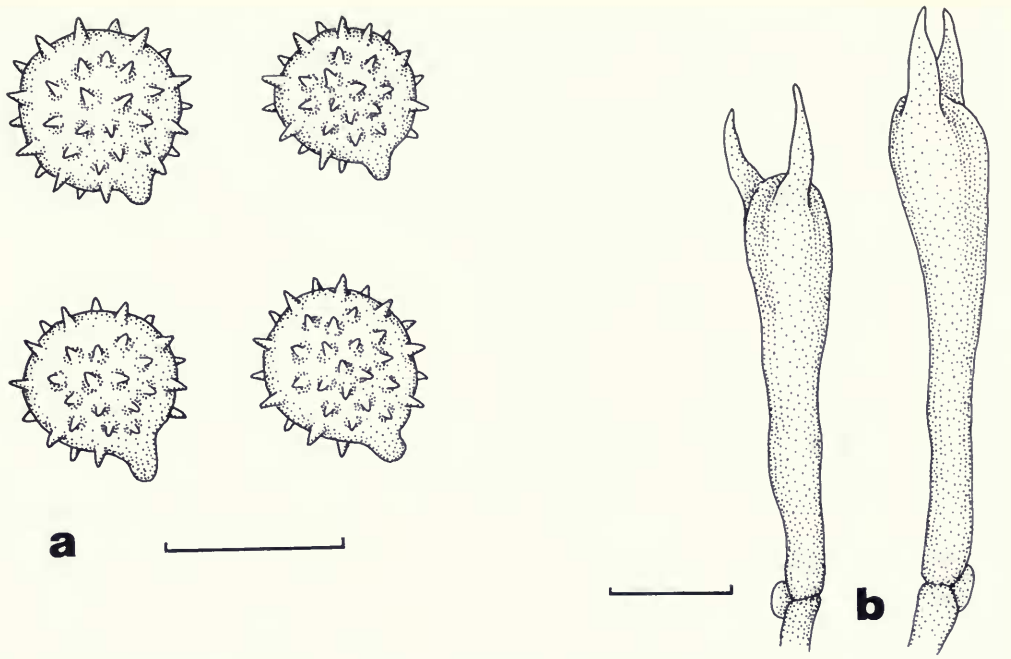


FIG. 18. Micromorphological features of *L. fraterna* (GMM 2126): **a,** basidiospores; **b,** bisterigmate basidia. Scale line = 10 μm.

rarely clavate, thin-walled, hyaline, only found in one collection. **Basidiospores** (excluding ornamentation) [120/6] (7.8–)8.5–14(–14.7) × (7–)8–12 μm ($\bar{x}$ = 9.4–12.6 × 8.5–10.5 μm), Q = 1–1.26(–1.33) ($\bar{Q}$ = 1.07–1.2), globose to broadly ellipsoid, occasionally ellipsoid, hyaline, echinulate; echinulae (0.5–)0.9–1.8 μm long, ≤ 1 μm wide at base, not crowded to crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–21 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

HABITAT AND DISTRIBUTION—Scattered to gregarious, occasionally caespitose; in poor soil, humus, or among mosses; under Pinaceae, *Betula,* or *Salix*; restricted to arctic, boreal, or montane habitats; common. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—*Laccaria montana* can be distinguished from *L. laccata* by having larger basidiospores and an arctic to boreal distribution.

The apparent stability of basidial characters within *Laccaria* coupled with the potential functional differences between 2-sterigmate taxa (facultative homothallism) versus 4-sterigmate taxa (obligatory heterothallism?) are the justification that I use to treat *L. montana* and *L. pumila* as separate species. Although there are differences in basidiospore size between these two taxa, these are probably due to the 4-sterigmate versus 2-sterigmate condition and are not independent character states.

Homokaryotic isolates from only two specimens of *L. montana* have been obtained to date. Repeated attempts to obtain either intra- or intercompatible pairings with isolates of either of these stocks have failed (Mueller, 1991c). Homokaryotic isolates of *L. pumila* have not been obtained, and consequently, no test of the putative genetic isolation between these two taxa has been undertaken. Multivariate morphometric analyses only loosely grouped together the two tested collections of *L. montana* (Mueller, 1991c). Finally, data are not available on potential genetic divergence between *L. montana* and other taxa because representatives of *L. montana* are not included in the RFLP analyses carried out by Gardes et al. (1990, 1991a).

Laccaria montana is among the more common *Laccaria* taxa found at high elevations and northern latitudes. At least some of the reports of *L. tetraspora* from the arctic are, according to their descriptions and illustrations, *L. montana* (e.g., Kobayasi et al., 1967; Miller et al., 1982).

FIG. 19. Basidiomata of *L. montana* (GMM 1250).

Laccaria pumila Fayod. Figures 21, 22, 54g, 70b.

≡ *Laccaria pumila* Fayod, Annali Accad. Agric. Torino 35: 91. 1893. TYPE: France, dept. Alpes maritimes, Col de la Cayolle, 2,500 m alt., 18 July 1976, *J. Trimbach 1463* (L!, neotype *fide* Mueller & Vellinga, 1986).
≡ *Clitocybe pumila* (Fayod) Saccardo, Syll. Fung. 17: 13. 1905.
≡ *Laccaria laccata* var. *pumila* (Fayod) Favre, Ergebn. Wiss. Unters. Schweiz. NatnParks V, 33: 51. 1955. [not validly published, basionym lacking].
= *Laccaria altaica* Singer, Bull. Soc. Mycol. France 83: 122. 1967.

Misapplied names: *Laccaria striatula sensu* Singer, Mycologia 35: 151. 1943; *sensu auct. plur.*—*Laccaria tortilis sensu* M. Lange, Meddel. Grønland 147: 29. 1955; *sensu* Miller et al., Mycologia 74: 583. 1982.

MACROMORPHOLOGY—**Pileus** 3–27(–40) mm broad, convex to plane, occasionally uplifted, often depressed, usually strongly translucent-striate when fresh, glabrous to finely fibrillose, occasionally becoming fibrillose-scaly with age, hygrophanous, red-brown to orange-brown ("Hay's Russet," "Burnt Sienna," or "Sanford's Brown"), fading to buff (near "Xanthine Orange," "Flesh-Ocher," or "Salmon-Buff"); margin incurved to decurved, often becoming plane, entire to undulate, occasionally eroded; context thin, concolorous. **Lamellae** sinuate to arcuate, distant, thick, waxy appearing, ≤ 8 mm broad, pinkish flesh color ("Flesh Color" or "Pale Flesh Color"). **Stipe** 4–61(–100) × 2–5(–9) mm, equal to subclavate, often slightly bulbous, occasionally caespitose, dry, fibrillose, longitudinally striate, ± concolorous with pileus, fading to ochraceous buff ("Amber Brown," "Flesh-Ocher," or "Apricot Buff"). **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–25 hyphae; terminal cells of fascicular hyphae 36.5–64 × 8–16 μm, filamentous, subclavate or clavate; walls up to 0.5 μm thick, light yellowish brown, often encrusted with pigment(s); contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel; hyphae mostly 3–18 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium**

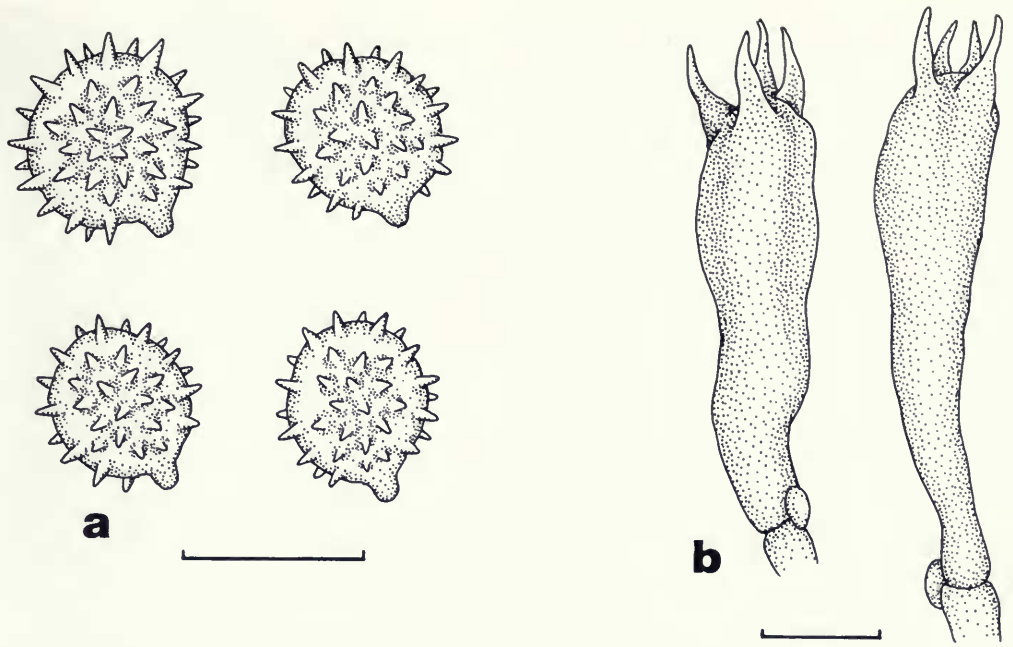


FIG. 20. Micromorphological features of *L. montana* (GMM 1813): **a**, basidiospores; **b**, tetrasterigmate basidia. Scale line = 10 μm.

morphologically undifferentiated. **Basidia** 37.5–64.5 × 10.5–16 μm, clavate, hyaline; sterigmata 2(–4), up to 14 μm long. **Cheilocystidia** 27.5–46 × 3 μm, filamentous to subclavate, hyaline, found in one collection only. **Basidiospores** (excluding ornamentation) [86/6] (10–)11–16.5(–20) × (7.8–)10–14.5(–16) μm ($\bar{x}$ = 12–13[–16.3] × 10.8–13.8 μm), Q = 1–1.29 ($\bar{Q}$ = 1.1–1.19), subglobose to broadly ellipsoid, occasionally globose or ellipsoid, hyaline, echinulate; echinulae < 0.5–1.4 (–1.8) μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–19 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

HABITAT AND DISTRIBUTION—Scattered to gregarious, occasionally caespitose; in poor soil, humus, or among mosses; under Pinaceae, *Betula*, or *Salix*; restricted to arctic, boreal, and montane regions; common. A list of collections examined is presented in Appendix A.

OBSERVATIONS—*Laccaria pumila* appears very similar in the field to *L. montana*, *L. tortilis*, and small striate forms of *L. laccata* var. *pallidifolia*. It can easily be distinguished, however, by its 2-sterigmate basidia that bear large, subglobose to broadly ellipsoid, echinulate basidiospores. *Laccaria pumila* has most commonly been reported under the name *L. altaica* Singer. As discussed by Mueller and Vellinga (1986), the name *L. pumila* has priority. Another name occasionally misapplied to this taxon is *L. striatula sensu* Singer *non* Peck (e.g., Singer, 1943b; Orton, 1960; Laursen & Chmielewski, 1982).

The major character distinguishing *L. pumila* from *L. montana* is that the latter has 4-sterigmate basidia. Both are restricted to arctic, subarctic, alpine, and boreal habitats and can be found growing sympatrically. Singer (1977) mentioned that *L. pumila* may only be a two-spored form of *L. montana* and thus the two might be conspecific. Lahaie (1981) and data accumulated during this study, however, have supported separation of these taxa at the species rank. In all specimens examined for this study, no basidiomata were found that had both 2- and 4-sterigmate basidia, and Lahaie (1981) only reported one collection in which both 2- and 4-sterigmate basidia were observed.

To date it has not been possible to obtain a tissue culture or to germinate the basidiospores of *L. pumila*.

Laccaria pumila appears to be the dominant, if not the exclusive, 2-sterigmate *Laccaria* found in the arctic, and the most common 2-sterigmate *Laccaria* found in the mountains of western United States. Lange (1955) and Kobayasi et al. (1967)

FIG. 21. Basidiomata of *L. pumila* (GMM 1298).

reported *L. tortilis* occurring in the arctic; however, the descriptions and illustrations of both indicate that the collections are probably *L. pumila.*

Laccaria striatula (Peck) Peck. Figures 23, 24, 55b, 71b.

≡ *Clitocybe laccata* var. *striatula* Peck, Annual Rep. New York State Bot. 48: 244. 1894. TYPE: USA, New York, Catskill Mountains, September, *C. H. Peck s.n.* (NYS!, holotype).
≡ *Laccaria striatula* (Peck) Peck, Annual Rep. New York State Bot. 157: 93. 1912.

MACROMORPHOLOGY—**Pileus** 6–30(–36) mm broad, convex, occasionally becoming plane, often depressed, strongly translucent-striate when fresh, occasionally plicate-striate, finely fibrillose, occasionally finely fibrillose-scaly near disc, hygrophanous, reddish brown to orange-brown ("Hazel," "Cinnamon-Rufous," or "Vinaceous-Rufous"), then lighter in color ("Salmon Color," "Seashell Pink," or "Pinkish Buff"); disc occasionally darker in color ("Hay's Russet"); margin incurved to decurved, becoming plane, entire to undulate; context thin, concolorous. **Lamellae** sinuate to adnate, close to subdistant to distant, relatively narrow to broad, thin to thick, pinkish flesh color ("Flesh-Ocher" or "Pale Flesh Color"). **Stipe** 20–70(–103) × 1–4(–8) mm, equal, occasionally slightly bulbous, glabrous, appearing cartilaginous when fresh, reddish brown, concolorous with disc or darker ("Kaiser Brown," "Hazel," "Cinnamon-Rufous," or "Onion-skin Pink"). **Basal mycelium** white.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with scattered to numerous small fascicles of ± perpendicular hyphae; fascicles usually composed of 5–15 hyphae; terminal cells of fascicular hyphae 33–85 × 6–18.5 μm, filamentous, subclavate, clavate, subcapitate, or ventricose-rostrate, occasionally strangulate; walls up to 0.5 μm thick, hyaline to light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 3–11(–27) μm diam., thin-walled, hyaline to light yellowish brown; cells filamentous to barrel-shaped. **Subhymenium** mor-

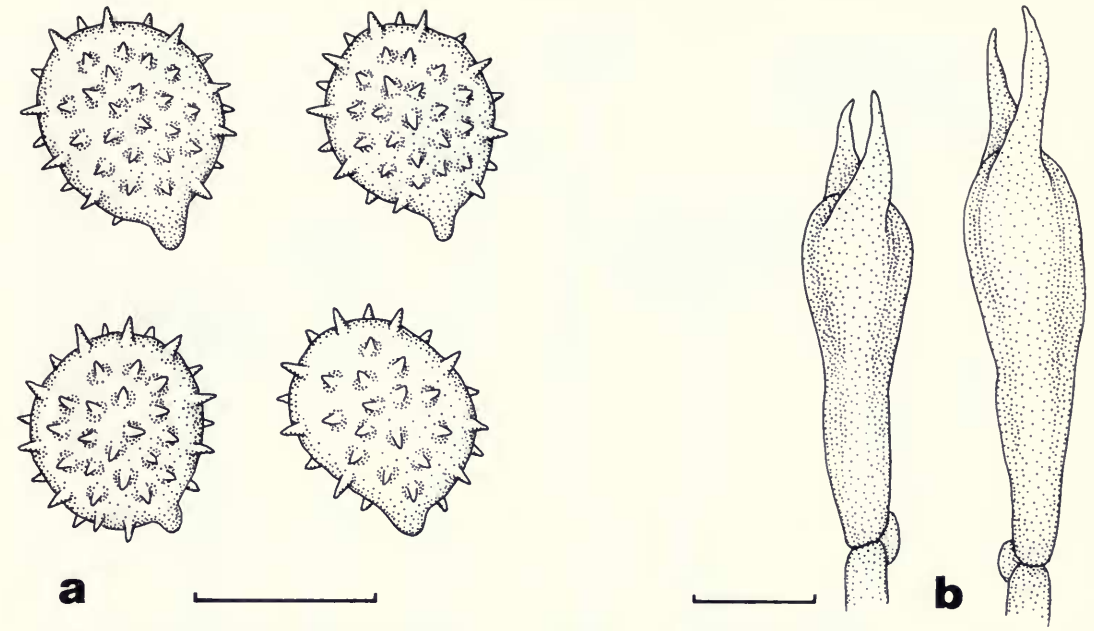


FIG. 22. Micromorphological features of *L. pumila* (GMM 1956): **a,** basidiospores; **b,** bisterigmate basidia. Scale line = 10 μm.

phologically undifferentiated. **Basidia** 30–59.5 × 8–14.5 μm, clavate, hyaline; sterigmata 4, up to 11 μm long. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) [265/13] 7–10(–12) × 7–10(–12) μm ($\bar{x}$ = 8–9[–10] × 7.7–9 [–10] μm), Q = 1(–1.12) ($\bar{Q}$ = 1–1.04), globose, rarely subglobose, hyaline, echinulate; echinulae 1.4–2.8 μm long, up to 1.8 μm wide at base, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–12.5 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

HABITAT AND DISTRIBUTION—Scattered to gregarious; in damp areas, often among wet mosses, usually not among *Sphagnum,* in mixed forests with *Tsuga canadensis* (L.) Carr. and/or other Pinaceae and Fagaceae, eastern North America. Material of this taxon has not been reported from Europe. In eastern North America it is common and abundant. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—*Laccaria striatula* is easily recognizable by its strongly translucent-striate pileus; long, gracile, glabrous, reddish brown stipe; and globose basidiospores with long and wide echinulae. These characteristics differentiate it from *L. laccata* var. *pallidifolia* and *L. ohiensis,* the two taxa to which it is phenetically most similar. Because of the difficulty of interpreting dried herbarium material lacking macromorphological notes, it is sometimes difficult to differentiate between material of *L. ohiensis* and *L. striatula.*

Tissue cultures of this taxon were not obtained, but homokaryotic isolates and reconstituted dikaryons were white and grew moderately fast on all employed media. Homokaryotic isolates of *L. striatula* were intersterile with tested isolates of other members of the *L. laccata* complex (Mueller, 1991c). Material of this taxon was not included in our RFLP analyses (Gardes et al., 1990, 1991a).

Singer (1946), Orton (1960), Bon (1983), and others have treated this name as referring to a taxon with bisterigmate basidia. An examination of the type specimen, however, showed it to have 4-sterigmate basidia, and that concept is used here (see Type Studies).

This taxon is abundant in wet mossy areas in the mountains of Georgia, North Carolina, New York, South Carolina, Tennessee, and Nova Scotia. It has also been collected in southern Ontario and northern Michigan and Wisconsin.

Mueller (1985) incorrectly used the name *L. glabripes* McNabb for this taxon. Aguirre-Acosta and Pérez-Silva (1978) reported *L. glabripes* from Mexico. Although I have not seen their material, it is likely that it is referable to *L. striatula,* not *L. glabripes.* All other reports of *L. glabripes* have

FIG. 23. Basidiomata of *L. striatula* (GMM 1780).

come from Australia and New Zealand. I have not encountered material of *L. striatula* among the specimens that I have collected and examined from Costa Rica and South America.

Laccaria ohiensis (Montagne) Singer. Figures 25, 26, 55a, 68b.

≡ *Agaricus ohiensis* Montagne, Syll. Crypt.: 100. 1856. TYPE: USA, Ohio, Columbus, before 1856, *Sullivant s.n.* (PC!, holotype).
≡ *Clitocybe ohiensis* (Montagne) Saccardo, Syll. Fung. V: 181. 1887.
≡ *Laccaria ohiensis* (Montagne) Singer, Mycologia 38: 688. 1946.
= *Clitocybe tortilis* var. *gracilis* Peck, Annual Rep. New York State Bot. 67: 36. 1903.
= *Laccaria tetraspora* Singer, Mycologia 38: 689. 1946.
≡ *Laccaria tetraspora* var. *tetraspora* Singer automatically established by var. *valdiviensis* Singer, Bull. Soc. Mycol. France 83: 113. 1967.
≡ *Laccaria tetraspora* var. *tetraspora* f. *tetraspora* Singer automatically established by f. *major* Singer, Bull. Soc. Mycol. France 83: 113. 1967.
= *Laccaria tetraspora* var. *valdiviensis* Singer, Bull. Soc. Mycol. France 83: 113. 1967.
= *Laccaria tetraspora* var. *peullensis* Singer, Bull. Soc. Mycol. France 83: 113. 1967.
= *Laccaria tetraspora* var. *scotica* Singer, Bull. Soc. Mycol. France 83: 114. 1967.
≡ *Laccaria scotica* (Singer) Bon, Doc. Mycol. 11: 23. 1981. [not validly published, basionym lacking].
= *Laccaria tetraspora* var. *xena* Singer, Bull. Soc. Mycol. France 83: 116. 1967.
= *Laccaria tetraspora* var. *aberrans* Singer, Bull. Soc. Mycol. France 83: 116. 1967.
= *Laccaria tetraspora* var. *tetraspora* f. *major* Singer, Bull. Soc. Mycol. France 83: 113. 1967.

MACROMORPHOLOGY—**Pileus** 7–26(–50) mm broad, convex to plane, often depressed, plicate-striate and strongly translucent-striate when fresh, glabrous to finely fibrillose, hygrophanous, reddish brown (near 8D6) soon becoming orange-brown (7C5–6), finally fading to buff; margin decurved to plane, entire to undulate; context thin, concolorous. **Lamellae** adnexed to adnate, distant, moderately thick, pinkish flesh color (6A2–7A3). **Stipe** 12–25(–40) × 1–2(–6) mm, equal or slightly bulbous, dry, glabrous to finely fibrillose, astriate to slightly longitudinally striate, concolorous with pileus. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–30 hyphae; terminal cells of fascicular hyphae 26–67 × 5–17.5 μm, filamentous, subclavate or clavate;

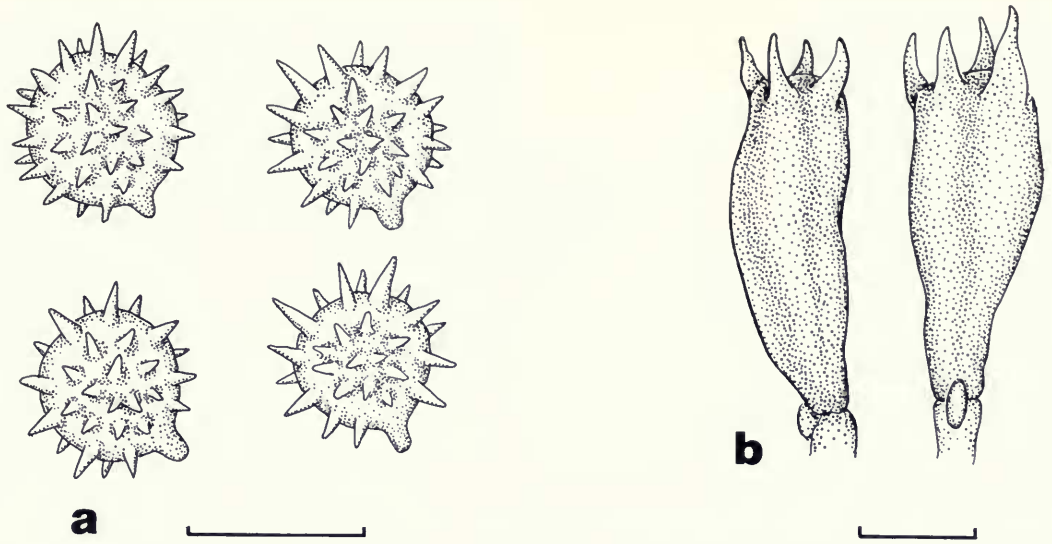


FIG. 24. Micromorphological features of *L. striatula* (GMM 1940): **a**, basidiospores; **b**, basidia. Scale line = 10 μm.

walls up to 0.5 μm thick, light yellowish brown, often encrusted with pigment(s); contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel; hyphae mostly 2–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 28–60 × 8–16 μm, clavate, hyaline; sterigmata 4, up to 10 μm long. **Cheilocystidia** 20–55 × 3–5.5 μm, filamentous to subcapitate, absent to relatively abundant, thin-walled, hyaline. **Basidiospores** (excluding ornamentation) [375/11] (6.4–)7.7–9.4 (–11) × (6.4–)7–9(–10.6) μm ($\bar{x}$ = 7.9–8.4[–9.3] × 7.8–8.4[–9.1] μm), Q = 1–1.09(–1.2) ($\bar{Q}$ = 1–1.05), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae (1–)1.5–2.8 μm long, > 1.2 μm wide at base, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate.

HABITAT AND DISTRIBUTION—Scattered to gregarious, not commonly collected in boreal or north temperate habitats. Commonly reported from subtropical, tropical, and south temperate regions. A list of collections examined is presented in Appendix A.

OBSERVATIONS—Collections of *Laccaria ohiensis* are characterized by their small basidioma size, strongly striate pilei, short, concolorous stipes, and globose basidiospores with long and wide echinulae.

Laccaria ohiensis is primarily differentiated from *Laccaria laccata* var. *pallidifolia* by having basidiospore echinulae that are ≥ 1.2 μm wide at their base. In contrast to *L. ohiensis,* whose collections are relatively uniform in macro- and micromorphological features, collections of *L. laccata* var. *pallidifolia* are highly variable in most morphological characters. Collections of *L. laccata* var. *pallidifolia* with small basidiomata and globose basidiospores (characteristics of *L. ohiensis*) are occasionally encountered.

Tested homokaryotic isolates of these two taxa are intersterile (Fries & Mueller, 1984; Mueller, 1991c) and differ in mtDNA and rDNA RFLP patterns (Gardes et al., 1990, 1991a; Mueller, 1991c). Isolates identified as belonging to mating group III (Fries & Mueller, 1984) and intersterility group 4 (Gardes et al., 1990, 1991a; Mueller, 1991c) are referable to *L. ohiensis.*

Laccaria ohiensis is differentiated from *L. striatula* by differences in macromorphology. Basidiomata of *L. striatula* have relatively long, glabrous stipes that are darker in color than the strongly striate pilei. Collections of these two taxa were not segregated during morphometric analyses of basidiospore characters (Mueller, 1991c), but tested isolates of the two taxa are intersterile. The isolate of *L. ohiensis* included in the analyses of mtDNA and rDNA had unique RFLP patterns (Gardes et al., 1990, 1991a).

The nolotype of *L. ohiensis* (see Type Studies) consists of basidiomata that have globose, echin-

FIG. 25. Basidiomata of *L. ohiensis* (GMM 1730).

ulate basidiospores born on 4-sterigmate basidia. This agrees with Singer's (1942) description of the type and Malençon's (1966) and Malençon and Bertult's (1975) concept of the taxon. In subsequent papers (e.g., Singer, 1946, 1977; Singer & Digilio, 1952; Bon, 1983), *L. ohiensis* was treated as a taxon with 2-sterigmate basidia. The correct name for the 2-sterigmate taxon discussed by Singer (1967, 1977), which has moderate-sized, subglobose basidiospores and normally occurs in warm and dry regions, often under *Eucalyptus,* is *L. fraterna. Laccaria impolita* is similar to *L. fraterna* but differs in macromorphology and association with north temperate trees (see Type Studies).

Laccaria tortilis (Bolton) Cooke. Figures 27–29, 55c,d, 72b.

≡ *Agaricus tortilis* Bolton, Hist. Fung. Halifax 1: 41, tab. XLI, fig. A. 1788. TYPE: Tab. XLI, fig. A in Bolton, Hist. Fung. Halifax vol. 1. 1788 (lectotype *fide* Mueller, 1991a). Representative specimen: Great Britain, Scotland, Yorkshire, Tanfield Lodge, 6 September 1969, *Orton 3642* (E!, "neotype" *fide* Mueller, 1987).

≡ *Omphalia tortilis* (Bolton) S. F. Gray, Nat. Arr. Brit. Pl. 1: 613. 1821.

≡ *Laccaria tortilis* (Bolton) Cooke, Grevillea 12: 70. 1884.

≡ *Clitocybe tortilis* (Bolton) Saccardo, Syll. Fung. 5: 198. 1887.

≡ *Collybia tortilis* (Bolton) Quélet, Flore Mycologique: 237. 1888.

≡ *Clitocybe laccata* var. *tortilis* (Bolton) Barla, Fl. mycol. ill.: 64. 1892.

= *Agaricus echinosporus* Spegazzini, Anales Soc. Ci. Argentina 10: 123. 1880.

≡ *Clitocybe echinospora* (Spegazzini) Saccardo, Syll. Fung. 5: 198. 1887.

≡ *Laccaria echinospora* (Spegazzini) Singer, Ann. Mycol. 41: 17. 1943.

= *Clitocybe revoluta* Barla, Fl. mycol. ill.: 64. 1888. [*non Clitocybe revoluta* Peck, Annual Rep. New York State Bot. 46: 23. 1893].

MACROMORPHOLOGY—**Pileus** 5–23 mm broad, convex, becoming plane to uplifted, strongly plicate-striate, subglabrous to finely fibrillose, hygrophanous, vinaceous brown to brownish orange ("Vinaceous-Brown," "Sorghum Brown," or "Orange Rufous") fading lighter in color ("Rood's Brown" to "Vinaceous-Russet"), eventually becoming buff color; margin plane, undulate, eroded,

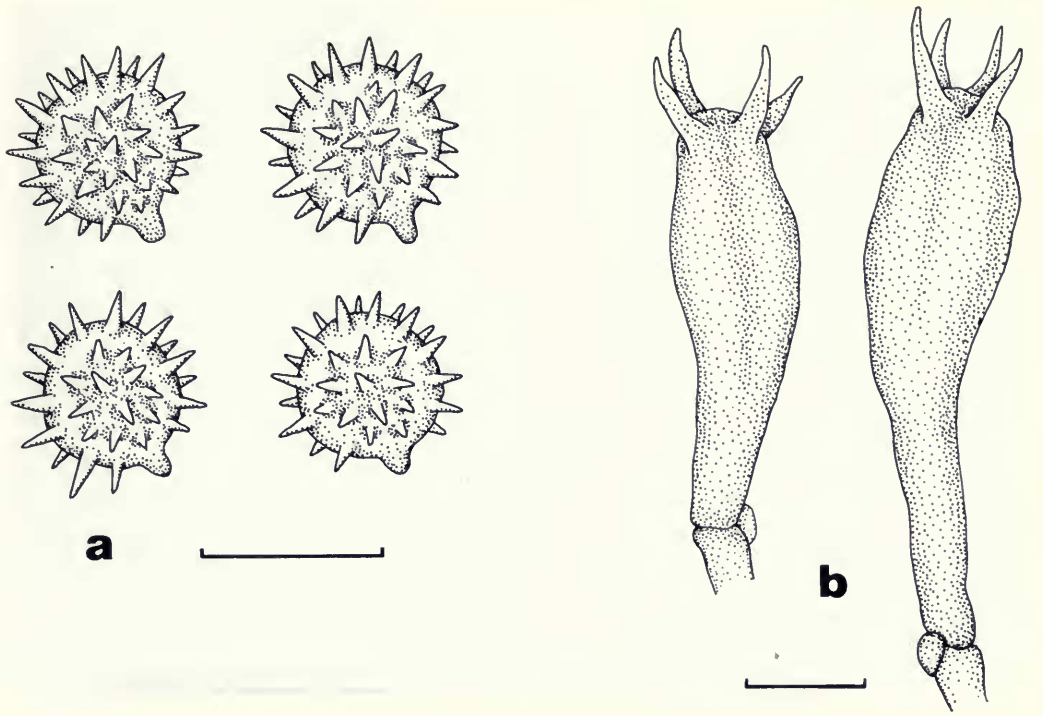


FIG. 26. Micromorphological features of *L. ohiensis* (GMM 2354): **a,** basidiospores; **b,** basidia. Scale line = 10 μm.

or rimose; context thin, concolorous. **Lamellae** sinuate to adnate, distant, broad, thick, pinkish flesh color to slightly vinaceous ("Flesh Color" to "Light Russet-Vinaceous"). **Stipe** 4–15 × 1–3.5 mm, equal to subbulbous, dry, finely fibrillose, not striate, concolorous with pileus. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–15 hyphae; terminal cells of fascicular hyphae 26.5–69 × 6.5–15 μm, filamentous to clavate; walls up to 0.5 μm thick, light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 6–14.5 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 33–64 × 7–16 μm, clavate, hyaline; sterigmata 2(3), up to 11.5 μm long. **Cheilocystidia** lacking or scarce; filamentous. **Basidiospores** (excluding ornamentation) [90/6] (9.2–)10–14.5(–16) × (8.3–)10–14.5 (–16) μm ($\bar{x}$ = 10.9–13 × 10.5–12.7 μm), Q = 1–1.09(–1.17) ($\bar{Q}$ = 1–1.03[–1.07]), globose, rarely subglobose, hyaline, strongly echinulate; echinulae 1.4–3.2(–4) μm long, up to 2.3 μm wide at base, crowded; hilar appendix 1.3–2.3 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** 3–14 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

HABITAT AND DISTRIBUTION—Scattered to gregarious, occasionally caespitose, often on bare, poorly drained soil, apparently associated with both Pinaceae and Fagaceae; cosmopolitan; not common. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—*Laccaria tortilis* can be distinguished from the rest of the small, plicate-striate *Laccaria* taxa by its 2-sterigmate basidia that bear large, globose basidiospores with long and broad echinulae.

It has not been possible to obtain tissue cultures or to germinate the basidiospores of this taxon. Material of *L. tortilis* was not included in the RFLP analyses of Gardes et al. (1990, 1991a).

There has been some confusion in the literature concerning the correct name for this taxon. *Agaricus tortilis* is the earliest name used for this mac-

FIG. 27. Basidiomata of *L. tortilis* (GMM 1710).

FIG. 28. Basidiomata of *L. tortilis* (GMM 1710).

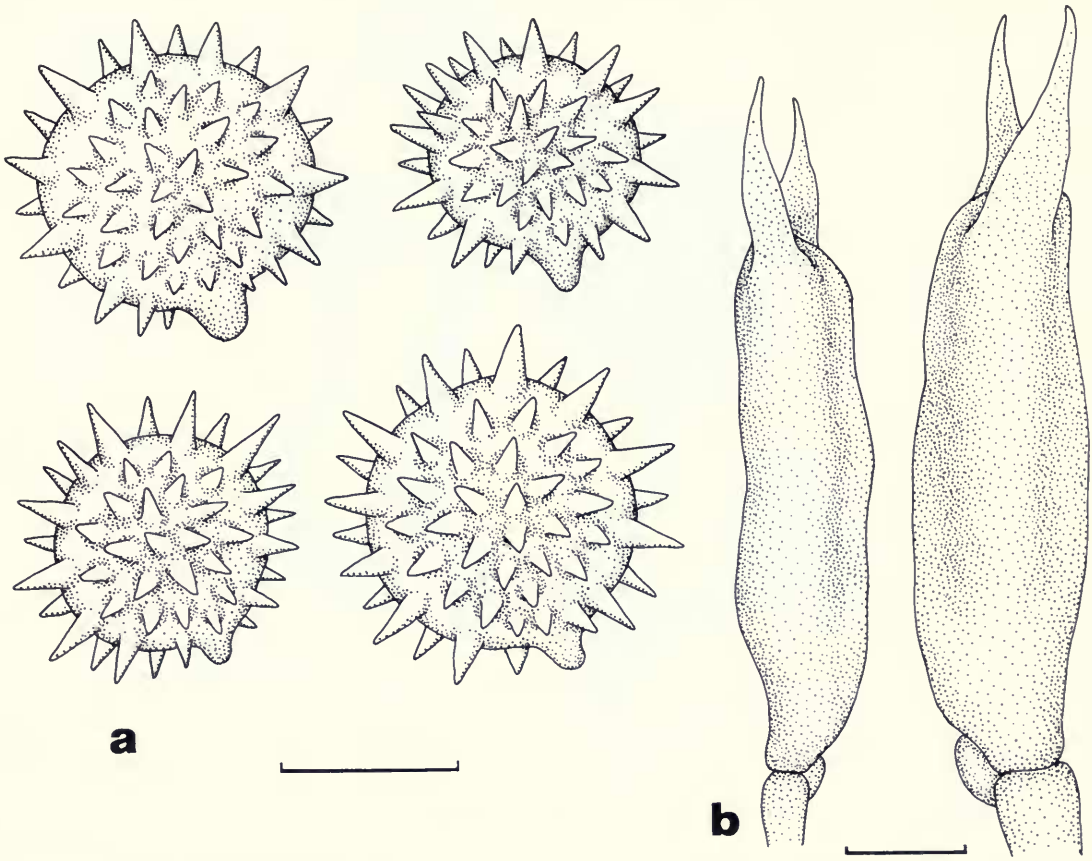


FIG. 29. Micromorphological features of *L. tortilis* (McAdoo 78#28): **a**, basidiospores; **b**, basidia. Scale line = 10 μm.

romorphological form (Bolton, 1788). Although no holotype exists, and Bolton's description did not give any morphological data, his color plate clearly illustrated the macromorphological traits of this taxon. I agree with the majority of modern workers (e.g., Dennis et al., 1960; Orton, 1960; Bon, 1983; Moser, 1983) who use the binomial *L. tortilis* for this taxon based on common usage (Korf, 1982a,b). Additionally, an examination of representative material from the environs of the type locality shows that Bolton probably had access to specimens that fit this micromorphological form. Rea (1922), Singer (1950a, 1952), Ballero and Contu (1989), and a few others consider *A. tortilis* to be a smaller-basidiospored species, and Singer (1943b, 1950a, 1952, 1967, 1977, 1986) used *L. echinospora* (Spegazzini) Singer for this taxon. Clémençon (1984) recognized both *L. tortilis* and *L. echinospora* as large-basidiospored taxa. He differentiated them on echinulae length, with *L. tortilis* having shorter echinulae than *L. echinospora.*

In an attempt to stabilize the application of the name, Mueller (1987) designated a neotype for *L. tortilis.* As discussed under *L. proxima,* the conflicting interpretations of this name have not been resolved by designating Bolton's illustration the lectotype. To stabilize the application of this epithet, the collection that was proposed as a neotype (Mueller, 1987) is now designated a "representative specimen" (see Type Studies).

In North American literature, Peck (1912) and Murrill (1914) used the name in the current sense, while Coker and Beardslee (1922) used *L. tortilis* for specimens with 4-sterigmate basidia and moderate-sized basidiospores.

Although not frequently collected, *Laccaria tortilis* occurs throughout much of the United States and Canada outside of arctic habitats. Most re-

FIG. 30. Basidiomata of *L. trichodermophora* (GMM 2321).

FIG. 31. Somatic culture mats of *L. trichodermophora* (GMM 1014). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.

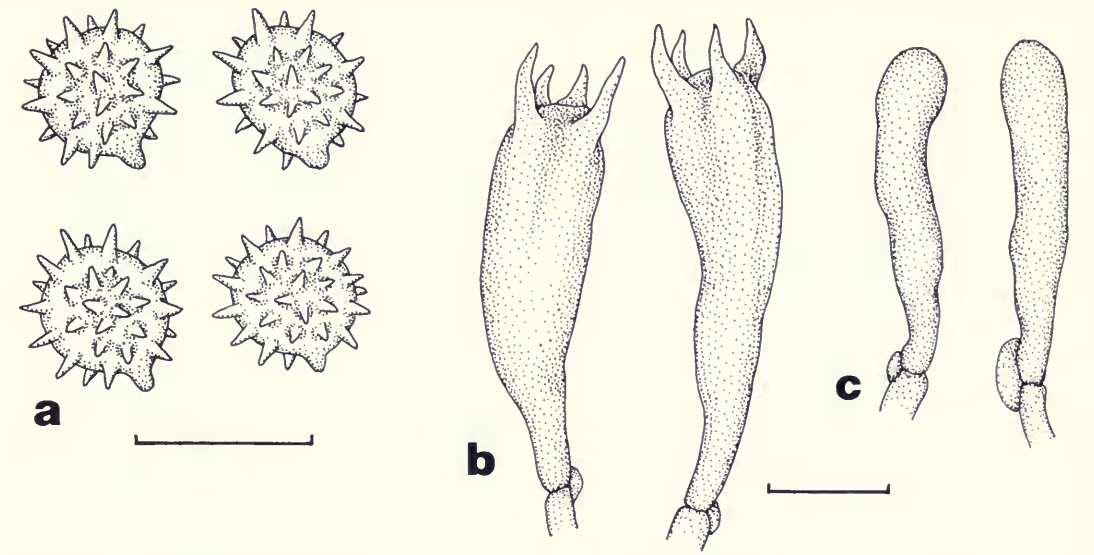


FIG. 32. Micromorphological features of *L. trichodermophora* (GMM 2306): **a**, basidiospores; **b**, basidia; **c**, cheilocystidia. Scale line = 10 μm.

ports under this name from the arctic refer to collections of *L. pumila* (see Observations under *L. pumila*).

Laccaria Metasection Amethystina
[see p. 24 for discussion]

Basidiomata and somatic culture mats with violet pigment(s); basidiospores not ellipsoid to oblong with echinulations 0.5(–1.4) μm long.

Laccaria trichodermophora G. M. Mueller. Figures 30–32, 56c, 72c.

Laccaria trichodermophora G. M. Mueller, Mycotaxon 20: 112–114. 1984. TYPE: USA, Mississippi, Harrison Co., DeSoto National Forest, Harrison Experimental Forest, Road H-6, 5 December 1980, *G. M. Mueller 1062* (TENN 42523) (TENN!, holotype).

Misapplied name: *Laccaria farinacea sensu* Singer *non* Hudson, Sydowia Beih. 7: 8. 1973.

MACROMORPHOLOGY—**Pileus** 9–66 mm broad, convex to plane, occasionally becoming uplifted, often depressed, not striate, strongly pruinose to fibrillose, becoming fibrillose-scaly to scaly owing to cuticular diffraction, hygrophanous, brownish orange, occasionally reddish brown ("Hazel," "Vinaceous-Rufous," "Auburn," "Orange Rufous," "Cacao Brown," or "Cinnamon-Rufous"), fading light brown to buff color ("Flesh-Ocher" to "Apricot Buff"), occasionally darker reddish brown at disc ("Hay's Russet" to "Kaiser Brown"); margin incurved, decurved, or plane, entire to undulate, occasionally becoming eroded; context 1–2 mm thick, tapering quickly to margin, pinkish flesh color ("Light Congo Pink" to "Pale Vinaceous-Pink"). **Lamellae** sinuate to adnate, close to distant, broad, relatively thin to thick, flesh color ("Vinaceous-Pink," "Shell Pink," "Flesh Color," or "Pale Salmon Color"), at times vinaceous in age (near "Vinaceous"). **Stipe** 20–115 × 2–11 mm, equal, subclavate or slightly bulbous, dry, fibrillose, inconspicuously to moderately longitudinally striate, concolorous with pileus; context stuffed, becoming hollow, concolorous with pileus context. **Basal mycelium** violet (near "Lavender" or "Pale Violet") when fresh, strongly hygrophanous, fading to white. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of very numerous large fascicles of ± perpendicular hyphae, often forming a trichodermium in young specimens and at the disc; fascicles composed of 15–30 or more hyphae; terminal cells of fasciculate hyphae 25–73.5 × 6–32 μm, filamentous, clavate or occasionally capitate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–18 μm diam., thin-walled, hyaline to light yellowish brown; cells fil-

amentous to barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 24.5–55 × 7–13(–20) μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Cheilocystidia** 17.5–60 × 2–6.5 μm, filamentous, occasionally subclavate, thin-walled, hyaline, absent, scattered or abundant. **Basidiospores** (excluding ornamentation) [415/20] (6.2–)6.8–8.7(–10.6) × 6–8(–9.2) μm ($\bar{x}$ = 7.1–8[–8.5] × 6.3–8 μm), Q = 1–1.24(–1.36) ($\bar{Q}$ = [1.01–]1.08–1.17), subglobose to broadly ellipsoid, occasionally globose or ellipsoid, hyaline, echinulate; echinulae (0.5–)0.9–1.8 μm long, irregularly spaced to crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–12 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

Somatic Culture Mat Morphology (N = 8; Appendix B)—**PDA: Radius** at week 3 = 15–38 mm or 42–45 mm, week 6 = (23–)29–59 mm or covering agar surface; **mat** felty, tightly interwoven, uniformly thick or with narrow, thicker dendritic strands radiating out from plug, tightly appressed to agar surface, normally forming pruinose aerial layer away from plug with time, not translucent, bright violet fading to violet, finally to light orange-brown near plug; aerial hyphae light grayish violet; **margin** 2–6 mm broad, subfelty, felty or silky, thin to thick, entire to uneven, light violet to white; **plug** dark violet, soon becoming light orange-brown; **hyphae** morphologically undifferentiated, occasionally subcoralloid or irregularly swollen. **MMN: Radius** at week 3 = 24–44 mm or 52–64 mm, week 6 = (43–)54–78 mm or agar surface covered; **mat** subfelty becoming felty or silky, thin to thick, with 2 or 3 narrow (2–3 mm), slightly thicker concentric zones or with slightly thicker, radially arranged, dendritic strands or uniformly thin, tightly appressed to agar surface, translucent, light violet, thicker zones somewhat darker; **margin** not well differentiated from mat, silky to subfelty, sinuate, light violet to white; **plug** concolorous with mat; **hyphae** same as in PDA. **MEA: Radius** at week 3 = 20–42 mm, week 6 = 38 mm or agar surface covered; **mat** silky to subfelty, thin or thick, occasionally thicker near plug, loosely interwoven or interwoven, tightly appressed to agar surface, translucent, white; **margin** not well differentiated from mat, silky to subfelty, entire to sulcate, white; **plug** white; **hyphae** morphologically undifferentiated, occasionally irregularly swollen.

Habitat and Distribution—Scattered to gregarious; commonly encountered in southeastern North America, in temperate coniferous or mixed coniferous–deciduous forests, apparently usually associated with species of *Pinus*. A list of specimens examined is presented in Appendix A.

Observations—*Laccaria trichodermophora* differs from *L. laccata* by having violet basal mycelium and smaller basidiospores. Its culture mat morphology differs by displaying a faster growth rate and violet coloration on PDA and MMN. Because of the ephemeral nature of the violet pigment in the basal mycelium and the slight overlap of basidiospore size and shape with those of *L. laccata* var. *pallidifolia*, it is occasionally difficult to differentiate between dried herbarium specimens of the two taxa.

Laccaria trichodermophora can be distinguished from *L. bicolor* and *L. nobilis* by its distribution, basidioma coloration, and scant basal mycelium. Additionally, the three taxa have distinct culture mat morphologies. *Laccaria bullulifera* Singer from Mexico is characterized by the occurrence of large, swollen cheilocystidia.

Mueller and Gardes (1991) summarized the results of intercollection pairing studies, phenetic analyses, and analyses of mtDNA and rDNA RFLPs for the *L. bicolor* complex. They concluded that collections of *L. trichodermophora* were well delimited from *L. bicolor* and *L. nobilis* (see Observations under *L. bicolor*). The concept of *L. trichodermophora* used here includes material termed Bi1 and *L. trichodermophora* in previously published phenetic analyses (Mueller, 1985).

Singer and Moser (1965) and Singer (1973, 1977, 1986) used the name *L. farinacea* for the taxon herein referred to as *L. trichodermophora*. No type exists for *A. farinaceus*, and Hudson (1798) listed *A. laccatus* under *A. farinaceus* implying that *A. farinaceus* was only a new name for *A. laccatus*. Fries (1821) placed *A. farinaceus* in synonymy under *A. laccatus* var. "a." In addition, neither Hudson nor Persoon (1801) mentioned the color of the basal mycelium in their description. It was necessary, therefore, to propose a new name for this taxon.

All of the collections of *L. trichodermophora* observed from the southeastern United States appeared to be associated with *Pinus*. *Laccaria trichodermophora* has not been reported from western or midwestern North America. To date, no material referable to *L. bicolor sensu stricto* or *L. nobilis* has been encountered in southeastern North America. Material from the northeastern United States or Atlantic Coast of Canada was not included in Mueller and Gardes (1991), and the oc-

currence of these three taxa in that area is not known. Collections of *L. bicolor sensu lato* are commonly collected in northeastern North America and are currently treated as *L. bicolor*. Aguirre-Acosta and Pérez-Silva (1978) and Montoya-Bello et al. (1987) reported *L. trichodermophora* (as *L. farinacea sensu* Singer) from Mexico. Mueller and Strack (unpubl.) have collected *L. trichodermophora* beneath Neotropical species of *Quercus* in Costa Rica.

Laccaria bicolor (Maire) Orton. Figures 33–35, 56a,b, 60c.

≡ *Laccaria laccata* var. *bicolor* Maire, Publ. Inst. Bot. Barcelona 3: 84. 1937. TYPE: Spain, Catalonia, Collado de Tosses, 7 October 1933 *Maire s.n.* (MPU!, holotype).
≡ *Laccaria proxima* var. *bicolor* (Maire) Kühner & Romagnesi, 1935. Flore Analytique des Champignons Superieurs: 131. 1935. [*nom. invalidum*, Art. 33: 2 ICBN].
≡ *Laccaria bicolor* (Maire) Orton, Trans. Brit. Mycol. Soc. 43: 177. 1960.
= *Laccaria laccata* var. *pseudobicolor* M. Bon *in* Bon & Haluwijn, Doc. Mycol. 12(46): 42. 1982.

MACROMORPHOLOGY—**Pileus** 8–70 mm broad, convex to plane, often depressed, not striate, finely fibrillose, fibrillose-scaly or occasionally scaly, hygrophanous, pinkish flesh color ("Walnut Brown," "Onion-skin Pink," "Kaiser Brown," or "Cinnamon-Rufous") fading to buff color ("Flesh Ocher," "Salmon Buff," or near "Pale Salmon Color"); margin decurved to plane, entire to undulate, often eroded; context thin, tapering quickly to margin, light vinaceous ("Pale Brownish Vinaceous" or "Hydrangea Pink"). **Lamellae** adnate to arcuate, subdistant to distant, broad, thick, light vinaceous ("Pale Purplish Vinaceous," "Pale Vinaceous," or "Hydrangea Pink"), fading to pinkish flesh color ("Light Congo Pink" or "Shell Pink"), then light flesh color ("Pale Flesh Color" or "Pale Salmon Color"). **Stipe** 23–85(–130) × 3–6(–10) mm, equal, subclavate or slightly bulbous, dry, fibrillose, longitudinally striate, concolorous with pileus; striations concolorous with ground color or slightly darker red brown. **Basal mycelium** copious, hygrophanous, violet when fresh ("Dull Lavender" to "Pale Vinaceous-Lilac"), becoming white.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with numerous large fascicles of ± perpendicular hyphae; fascicles composed of (15–)25–30 or more hyphae; terminal cells of fascicular hyphae 27.5–76 × 6–18.5 μm, subclavate, clavate, or rarely subcapitate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline to light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 2–13.5 μm diam., thin-walled, hyaline to light yellowish brown; cells filamentous to barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 28.5–55 × 7.4–13 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Cheilocystidia** 24.5–55 × 2.5–8 μm, filamentous to subclavate, thin-walled, hyaline, absent to abundant. **Basidiospores** (excluding ornamentation) [465/28] (5.5–)7–8.7(–10) × (5.5–)6–7.8(–9.2) μm ($\bar{x}$ = 7.0–8.4[–9] × 6.2–7.8 μm), Q = 1–1.26(–1.36) ($\bar{Q}$ = 1.05–1.23), subglobose to broadly ellipsoid, occasionally globose or ellipsoid, hyaline, echinulate; echinulae 1–1.8 μm long, ≤ 1 μm wide at base; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–15.5 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

SOMATIC CULTURE MAT MORPHOLOGY (N = 10; Appendix B)—**PDA: Radius** at week 3 = 11–32 mm, week 6 = 18–40(–54) mm; **mat** felty, thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, occasionally becoming furrowed owing to irregular infolding near plug, not translucent, bright violet fading to light orange-brown or remaining bright violet; aerial hyphae light grayish violet, often covering most of mat by week 6 and then masking mat color; **margin** 3–4 mm broad, subfelty, thin, light violet to white; **plug** dark violet at first, becoming light orange-brown; **hyphae** morphologically undifferentiated or irregularly swollen, violet in mass, pigment intracellular. **MMN: Radius** at week 3 = 22–41 mm, week 6 = (31–)40–63 mm; **mat** silky, subfelty or felty, thin or thick, loosely to tightly interwoven, occasionally with 3 or 4 narrow concentric thicker bands, tightly appressed to agar surface, translucent or not translucent, at first light violet or violet, soon buff, by week 3 violet color usually restricted to thicker bands and near margin; **margin** 2–4 mm broad, silky to subfelty, thin, loosely interwoven, even to serrate, light violet; **plug** light violet; **hyphae** morphologically undifferentiated or rarely irregularly swollen. **MEA: Radius** at week 3 = 19–43 mm, week 6 = 30–52 mm, TENN 42529 68–76 mm; **mat** subfelty to felty, thick, interwoven, occasionally with small, scattered, thicker sectors, tightly appressed to agar surface, translucent, white;

FIG. 33. Basidiomata of *L. bicolor* (GMM 1327).

FIG. 34. Somatic culture mats of *L. bicolor* (GMM 1293). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.

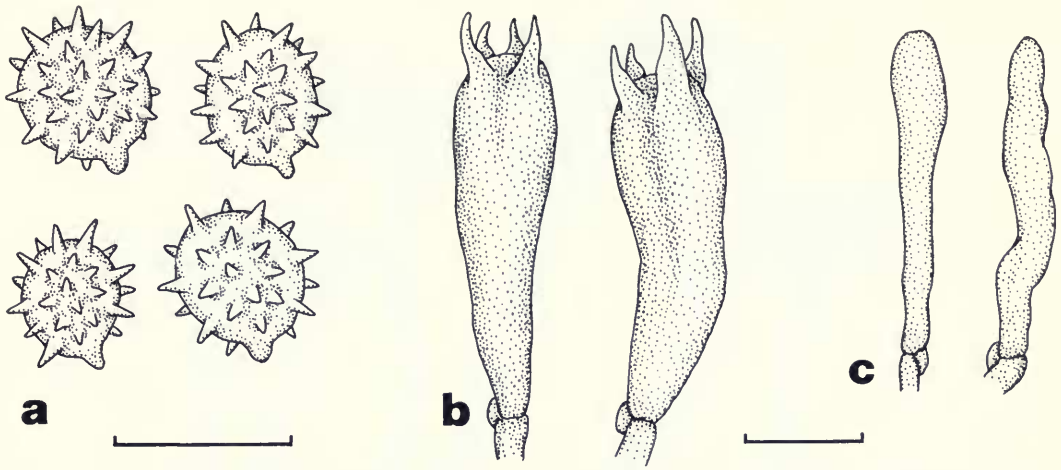


FIG. 35. Micromorphological features of *L. bicolor* (GMM 2013): **a,** basidiospores; **b,** basidia; **c,** cheilocystidia. Scale line = 10 μm.

margin 2–3 mm broad, subfelty, not well differentiated, often very uneven, white; plug white; **hyphae** morphologically undifferentiated, occasionally with a few scattered irregular swollen hyphae.

HABITAT AND DISTRIBUTION—Scattered, occasionally caespitose. Very commonly encountered on soil or among mosses under conifers in western North America east to Ontario and Michigan. Specimens of *L. bicolor sensu lato* from northeastern United States and the Atlantic provinces of Canada are included under *L. bicolor* (see below). A list of specimens examined is provided in Appendix A.

OBSERVATIONS—*Laccaria bicolor* is characterized by having moderate-sized basidiomata, violaceous lamellae when fresh, and copious violet mycelium at the stipe base. *Laccaria trichodermophora* differs by having pinkish flesh-colored lamellae and sparse, strongly hygrophanous, violet basal mycelium. *Laccaria bicolor* has been reported from western and northern North America and Europe; *L. trichodermophora* has only been reported from southeastern North America, Mexico, and Costa Rica. The large, scaly basidiomata of *L. nobilis* differentiate that taxon from *L. bicolor*. *Laccaria nobilis* occurs sympatrically with *L. bicolor* in western and north central North America but has not been reported from Europe. All three of these taxa have distinct culture mat morphologies.

Mueller and Gardes (1991) summarized the results of intercollection pairing studies, phenetic analyses, and analyses of mtDNA and rDNA for the *L. bicolor* complex. Three intersterility groups were detected among 38 North American isolates tested. Matings within a group were frequent but mating between intersterility groups were rare. The three intersterility groups were delimited during phenetic analyses, indicating that these groups differed morphologically. The two Swedish isolates used were completely intercompatible with one North American group but only partially intercompatible with isolates of the other two groups. These results were more or less concordant with data obtained by RFLP analysis of mtDNA and rDNA (Gardes et al., 1990, 1991a). The North American isolates formed a relatively homogeneous group and were differentiated from the two Swedish isolates based on analyses of rDNA (Gardes et al., 1990). In contrast, analyses of mtDNA detected divergence between the North American intersterility groups but not between the Swedish isolates and North American isolates (Gardes et al., 1991a). Based on a synthesis of these data, the Swedish collections and material from western North America and areas adjacent to the Great Lakes were treated as *Laccaria bicolor sensu stricto*; *L. nobilis* was circumscribed as a taxon with large, robust, scaly basidiomata occurring sympatrically with North American material of *L. bicolor*; and material from the southeastern United States with pinkish flesh-colored lamellae was treated as *L. trichodermophora* (Mueller & Gardes, 1991).

Laccaria bicolor is one of the most common *Laccaria* taxa found in the coniferous forests of

FIG. 36. Basidiomata of *L. nobilis* (GMM 2048).

FIG. 37. Somatic culture mats of *L. nobilis* (GMM 1205). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.

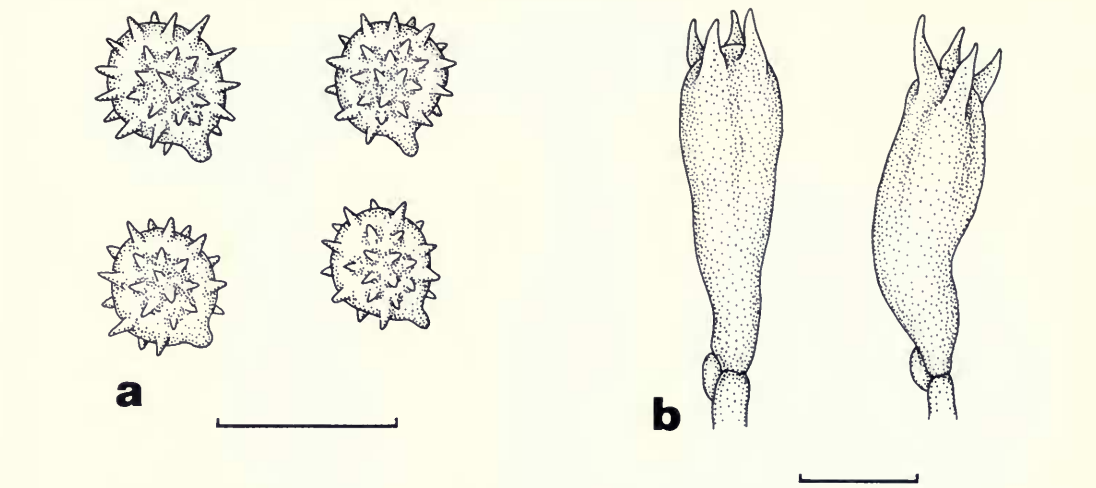


FIG. 38. Micromorphological features of *L. nobilis* (GMM 2048): **a,** basidiospores; **b,** basidia. Scale line = 10 μm.

western North America and the Great Lakes area. Collections of *L. bicolor sensu stricto* were not encountered from the southeastern United States. Material of *L. bicolor sensu lato* from the northeastern United States or Atlantic provinces of Canada, although frequently encountered, was not available to include in the studies of Mueller and Gardes (1991). Consequently, the occurrence and distribution of these three species in that area are unknown, and collections of *L. bicolor sensu lato* from this region have been treated as *L. bicolor* in this monograph.

Isolates of *L. bicolor* are very frequently used in applied studies on ectomycorrhizae (Kropp & Langlois, 1990).

Laccaria nobilis Smith *apud* G. M. Mueller. Figures 36–38, 56d,e, 67c.

Laccaria nobilis Smith *apud* G. M. Mueller, Mycotaxon 20: 105–108. 1984. [*Laccaria nobilis* Smith, *nom. herb.*]. TYPE: USA, Colorado, Larimer Co., Roosevelt National Forest, Rayah Wilderness, Blue Lake Trail, 13 September 1981, *G. M. Mueller 1198* (TENN 42527) (TENN!, holotype).

MACROMORPHOLOGY—**Pileus** 16–85 mm broad, convex to plane, occasionally becoming uplifted, depressed to deeply depressed, not striate, fibrillose-scaly becoming scaly to squarrose, reddish brown (8C7–8D7) to brownish orange ("Sanford's Brown" or "Cinnamon-Rufous") 6C7, 7C6–7D7), occasionally darker at disc ("Hazel"); margin incurved, decurved or plane, occasionally upturned, entire to eroded; context thin, concolorous with lamellae. **Lamellae** sinuate to adnate, close to distant, thick, vinaceous (8B2–9B3) to pinkish flesh color ("Flesh Color," "Pale Flesh Color," or "Orange-Pink") (7A2–7A3). **Stipe** (21–)26–110(–160) × 4–10(–16) mm, equal, slightly bulbous or subclavate, dry, fibrillose, with prominent longitudinal striations or reticulate ridges, often with apical recurved scales at maturity, concolorous with pileus; striations concolorous with stipe ground color or somewhat darker reddish brown. **Basal mycelium** violet, soon becoming white. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 or more hyphae; terminal cells of fascicular hyphae 34.5–75 × 4–19 μm, subclavate, clavate, broadly clavate or capitate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 32–55 × 8–14 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Cheilocystidia** lacking. **Basidiospores** (excluding ornamentation) [122/8] (6.2–)6.6–9.7(–10.6) × (5–)6.2–8.7 μm ($\bar{x}$ = [7–]7.4–8.8 × [6–]6.3–7.8 μm), Q = 1–1.26(–1.39) ($\bar{Q}$ = [1.03–]1.16–1.22), subglobose to broadly ellipsoid, occasionally globose or ellipsoid, hyaline, echinulate; echinulae 0.5–1.4 μm long ($\bar{x}$ = 0.9 ±

FIG. 39. Basidiomata of *L. trullissata* (GMM 3048).

FIG. 40. Habitat view of *L. trullissata* (GMM 3048) illustrating typical growth in sand.

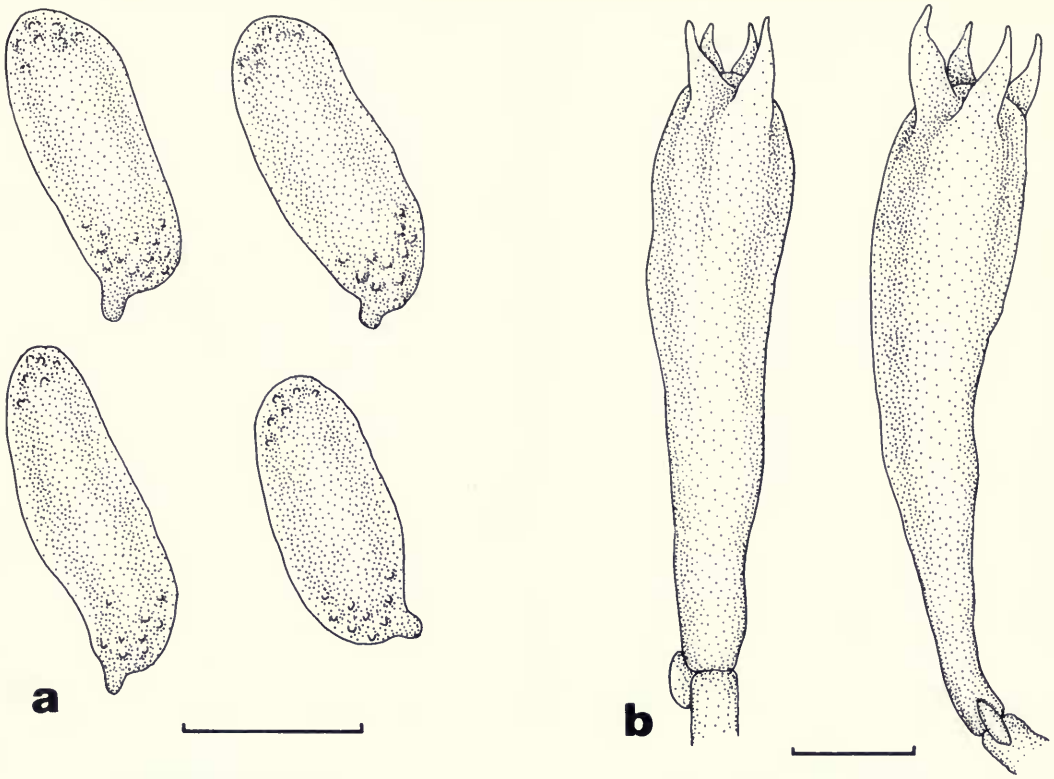


FIG. 41. Micromorphological features of *L. trullissata* (GMM 1914): **a**, basidiospores; **b**, basidia. Scale line = 10 μm.

0.2 μm), crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–12 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

SOMATIC CULTURE MAT MORPHOLOGY (N = 2; Appendix B)—**PDA: Radius** at week 3 = 23–31 mm, week 6 = 35–43 mm; **mat** felty, thick, tightly interwoven, almost crustose, tightly appressed to agar surface, with time forming pruinose aerial layer away from plug, not translucent, at first bright violet, by week 6 violet color restricted to a 7–9 mm band near margin, rest of mat light orange-brown; pruinose aerial hyphae light grayish purple becoming light orange-brown; **margin** 3–4 mm broad, subfelty, thin, uneven, light violet to white, **plug** concolorous with mat; **hyphae** morphologically undifferentiated, occasionally irregularly swollen, purplish brown in mass. **MMN: Radius** at week 3 = 40–47 mm, week 6 = 67–78 mm; **mat** subfelty, thin, slightly thicker with age, loosely to tightly interwoven, tightly appressed to agar surface, translucent, light violet, in time color restricted to 3–4 mm band at midpoint, remainder of mat white; **margin** 3–6 mm broad, silky to subfelty, thin, parallel to loosely interwoven, entire, light violet to white; **plug** concolorous with mat; **hyphae** morphologically undifferentiated, rarely irregularly swollen near margin. **MEA: Radius** at week 3 = 33–47 mm, week 6 = 47–77 mm; **mat** subfelty, thin to slightly thicker near plug, loosely interwoven, tightly appressed to agar surface, translucent, white; **margin** 1–2 mm broad, subfelty, thinner than mat, undulate; **hyphae** morphologically undifferentiated.

HABITAT AND DISTRIBUTION—Solitary to scattered. Infrequently encountered under Pinaceae in western North America and areas adjacent to the Great Lakes. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—*Laccaria nobilis* can be distinguished easily from other members of the *L. bicolor* complex by its large size, scaly to squarrose pileus, scaly stipe, and lack of obvious cheilocystidia. A. H. Smith proposed the name in an unpublished manuscript along with several other taxa, including *L. pisciodorus nom. prov.* (Smith no. 18812) and *L. sphagnicola nom. prov.* (Smith no.

4573). The latter two taxa were not judged sufficiently distinct, based on available material, to justify valid publication as discrete taxa.

The concept of *L. nobilis* used here has been broadened from that originally published by Mueller (1984, 1985). Interpretation of lamellae and basal mycelium colors was difficult in many of the collections included in the original description because the specimens were mature and weathered. Additional material was collected subsequently that differed from the original collections in having vinaceous lamellae and violet mycelium at the base of the stipe. Because all of these collections had large, robust basidiomata that became quite scaly in age, strongly striate to nearly reticulate stipes, and similar micromorphology and somatic culture mat morphology, they were treated as a single taxon, *L. nobilis*. Isolates of more recently collected specimens were included among the material studied by Mueller and Gardes (1991).

Laccaria nobilis is well delimited from *L. bicolor* and *L. trichodermophora* based on intercollection pairing studies, phenetic analyses, and analyses of mtDNA and rDNA RFLPs (Mueller & Gardes, 1991) (see Observations under *L. bicolor*).

Laccaria nobilis has been identified among material collected throughout much of western North America (e.g., California, Colorado, Idaho, New Mexico, Oregon, and Washington) and from Michigan and Ontario.

Laccaria trullissata (Ellis) Peck. Figures 39–41, 57b–d, 72d.

≡ *Agaricus trullissatus* Ellis, Bull. Torrey Bot. Club 5: 45. 1874. TYPE: USA, New Jersey, Newfield, no date, *Ellis s.n.* (NYS!, lectotype *fide* Mueller, 1987).
≡ *Clitocybe trullissata* (Ellis) Saccardo, Syll. Fung. 5: 195. 1887.
≡ *Laccaria trullissata* (Ellis) Peck, Annual Rep. New York State Bot. 157: 90. 1912.

MACROMORPHOLOGY—**Pileus** 17–72 mm broad, convex to plane, occasionally depressed, not striate, fibrillose to fibrillose-scaly, grayish purple when very young (near 17B4), soon becoming red-brown, brown or buff ("Fawn Color," "Avellaneous," "Vinaceous-Buff," "Pale Vinaceous-Fawn," or "Pinkish Buff") (6A4–5, 6B6, 7D7 or 7E5–7); margin incurved to decurved, entire to eroded; context tapering to margin, pale purple (near "Light Vinaceous-Gray"). **Lamellae** adnate to arcuate, close to subdistant, narrow to moderately broad, thick, waxy appearing, dark violaceous ("Dark Heliotrope Gray" or "Deep Vinaceous-Gray"). **Stipe** 40–93 × 6–23 mm, subclavate to clavate, dry, fibrillose, longitudinally striate, covered with sand, occasionally with outer "cortical" layer splitting near apex, concolorous with pileus; context solid, concolorous with pileus context. **Basal mycelium** violaceous. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–25 hyphae; terminal cells 33.5–85 × 7–16 μm, subclavate, clavate, broadly clavate or capitate, walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–17 μm diam., hyaline, light yellowish brown or light vinaceous color; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 30–64.5 × 9–16 μm, clavate, hyaline; sterigmata 4, up to 10 μm long. **Cheilocystidia** lacking or very scarce and filamentous. **Basidiospores** [75/5] (13.3–)13.8–20.2(–21.6) × 5.5–8.3 μm ($\bar{x}$ = 15.3–17.3 × 6–7.3 μm), Q = 1.83–3.31 ($\bar{Q}$ = 2.37–2.51), subfusiform to fusiform-ellipsoid, hyaline, very finely roughened, not echinulate; hilar appendix 1.3–2 μm long, prominent, truncate; contents occasionally uniguttulate, rarely biguttulate. **Basal mycelium hyphae** 3–15.5 μm diam., tightly interwoven, hyaline; cells filamentous or barrel-shaped.

HABITAT AND DISTRIBUTION—Solitary to scattered; sand dunes or very sandy soil; usually associated with species of *Pinus*, eastern and midwestern North America. A list of specimens examined is provided in Appendix A.

OBSERVATIONS—*Laccaria trullissata* is distinguished from other North American *Laccaria* taxa by its habitat, macromorphology, and basidiospore characteristics. Collections of *Laccaria maritima* differ from those of *L. trullissata* in having shorter, less elongate, echinulate basidiospores.

Ectomycorrhizae were synthesized between one isolate of *L. trullissata* and seedlings of *Pinus resinosa* Ait. (unpubl. data). Intrastock pairings demonstrated that *L. trullissata* has a bifactorial compatibility system as do all other tested *Laccaria*.

Laccaria trullissata occurs in sandy areas along the eastern coast of North America, ranging from the Maritime Provinces of Canada to North and South Carolina along the Atlantic coast and Florida to Mississippi along the Gulf of Mexico. It can be encountered also in northcentral United States

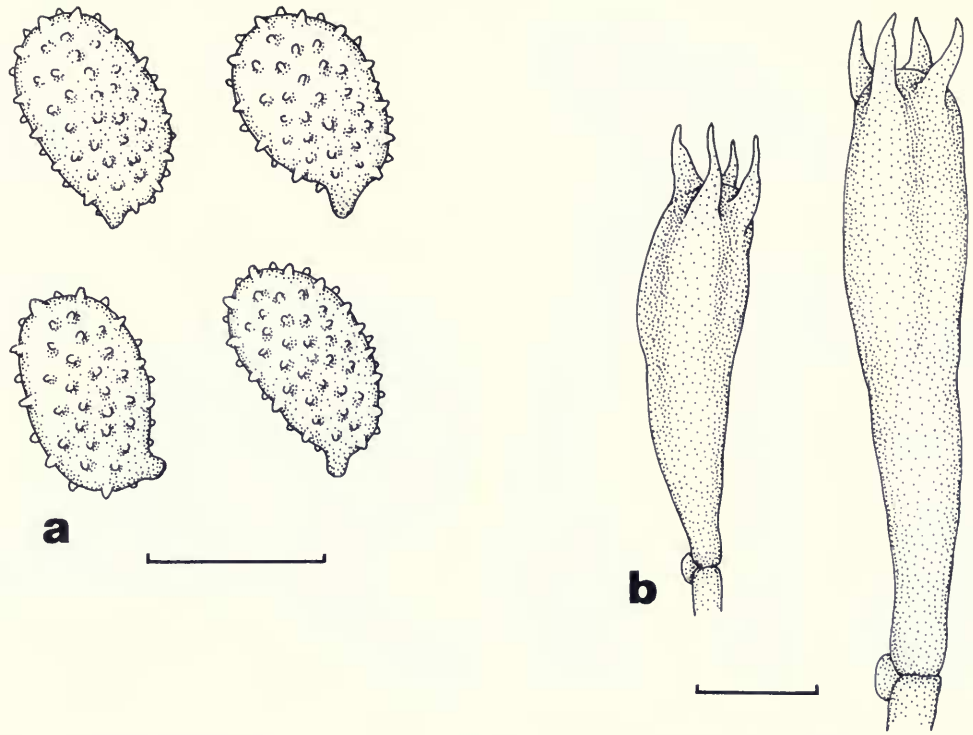


FIG. 42. Micromorphological features of *L. maritima* (DAOM 159709): **a**, basidiospores; **b**, basidia. Scale line = 10 μm.

and southcentral Canada in sand dunes along the Great lakes.

Laccaria maritima (Teodorowicz) Singer *ex* Huhtinen. Figures 42, 57a.

≡ *Hygrophorus maritimus* Teodorowicz, Grzyby wyzsze polskiego wybrzeza, Towarzystwo naukowe w Toruniu Badania Przyrodnicze Pomorskie 2: 31. 1936. TYPE: Fig. 5 in Teodorowicz, Grzyby wyzsze polskiego wybrzeza, Towarzystwo naukowe w Toruniu Badania Przyrodnicze Pomorskie 2: 31. 1936. (lectotype *fide* Mueller, 1991a).

≡ *Laccaria trullissata* (Ellis) Peck subsp. *maritima* (Teod.) Andersson, Bot. Not. Suppl. 2: 33. 1950.

≡ *Laccaria maritima* (Teodorowicz) Singer, Sydowia 15: 133. 1961. [not validly published, basionym lacking].

≡ *Laccaria maritima* (Teodorowicz) Singer *ex* Huhtinen, Fungi Canad. 319. 1987.

= *Laccaria trullissata* (Ellis) Peck forma *rugulospora* M. Lange, Meddel. Grønland 147: 30. 1955.

MACROMORPHOLOGY—**Pileus** up to 45 mm broad, convex to plane, becoming uplifted, often depressed, nonstriate or translucent-striate when fresh, glabrous to finely fibrillose, slightly viscid, hygrophanous, dark reddish brown to reddish orange-brown. **Lamellae** adnate to subdecurrent, distant, thick, broad, pinkish flesh color to vinaceous. **Stipe** large and robust, equal to clavate, dry, mostly covered with sand, concolorous with pileus. **Basal mycelium** off-white, hard to determine because of adhering sand. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with scattered ± perpendicular individual hyphae or fascicles of hyphae, terminal cells of hyphae 35–55 × 4–10 μm, hyaline. **Basidia** 37–60 × 9–15.5 μm, clavate, 4-sterigmate. **Cheilocystidia** none seen. **Basidiospores** (excluding ornamentation) [105/4] (10–)11.5–17(–19.5) × (5.5–)7.5–9.5(–10) μm ($\bar{x}$ = 13.3–15.4 × 8–8.5 μm), Q = 1.43–2(–2.17) ($\bar{Q}$ = 1.67–1.81), oblong to subfusiform, echinulate; echinulae 0.2–0.5 μm long.

HABITAT AND DISTRIBUTION—Scattered to gregarious; terrestrial, in sand including dunes; with or without apparent ectomycorrhizal associate. Only reported from a few sites in eastern Canada.

FIG. 43. Basidiomata of *L. ochropurpurea* (GMM 919). Largest pileus = 8 cm diam.

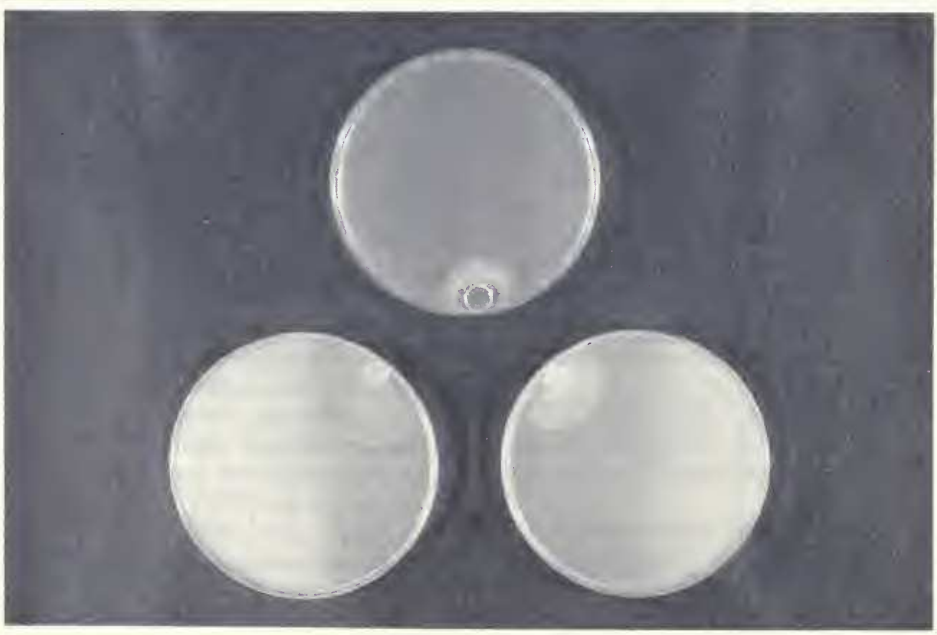


FIG. 44. Somatic culture mats of *L. ochropurpurea* (GMM 1015). Top on PDA, left on MMN, and right on MEA. Photo taken during week 4.

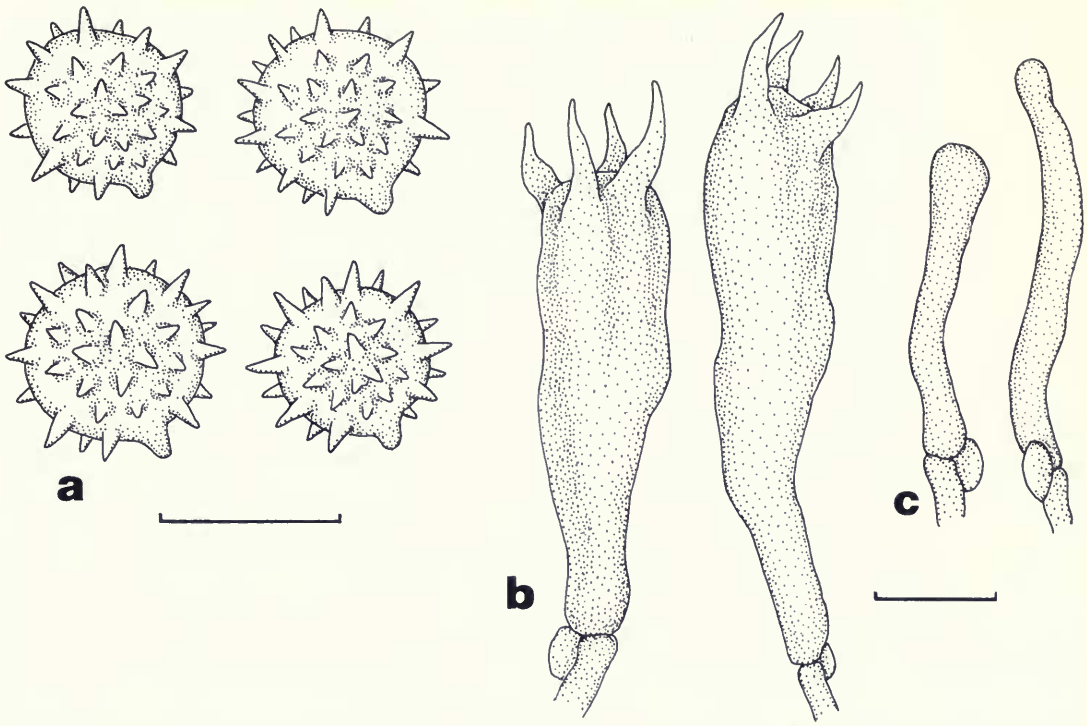


FIG. 45. Micromorphological features of *L. ochropurpurea* (E. Farwell 5074): **a,** basidiospores; **b,** basidia; **c,** cheilocystidia. Scale line = 10 μm.

Known primarily from northern Europe. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—*Laccaria maritima* is characterized by its restricted habitat, dark reddish brown pileus color, vinaceous-tinged lamellae, stipe buried in sand, and elongate, finely echinulate basidiospores. Collections of *L. trullissata* have larger basidiomata with deep violet lamellae and larger, more elongate (mostly 14–21.5 × 5.5–9 μm), finely roughened, not echinulate basidiospores.

It has not yet been possible to obtain a tissue culture or germinate the basidiospores of this taxon. Lack of cultures has prevented attempts at in vitro ectomycorrhizal synthesis to determine the ability of this taxon to form ectomycorrhizae with putative hosts.

This species has been reported from both coastal and inland dunes of northern Europe, the Netherlands, and Greenland (e.g., Teodorowicz, 1936; Andersson, 1950; Lange, 1955; Singer, 1961; Kallio & Heikkilä, 1963; Høiland, 1976; Vellinga, 1982). Huhtinen (1987) reports it for the first time from North America, where *L. trullissata* is found much more commonly in sand dunes than *Laccaria maritima.*

Laccaria ochropurpurea (Berkeley) Peck. Figures 43–45, 58d, 68a.

≡ *Agaricus ochropurpureus* Berkeley, London J. Bot. 4: 299–300. 1845. TYPE: USA, Ohio, Cincinnati, no date, *Lea 261* (K!, holotype).
≡ *Clitocybe ochropurpurea* (Berkeley) Saccardo, Syll. Fung. 5: 148. 1887.
≡ *Laccaria ochropurpurea* (Berkeley) Peck, Annual Rep. New York State Bot. 116: 41. 1907.
≡ *Clitocybe laccata* f. *major* Bresadola, Ann. Mycol. 18: 65. 1920.

MACROMORPHOLOGY—**Pileus** 35–100(–125) mm broad, obtuse, convex, plane or uplifted, often depressed, not striate, dry, subglabrous, finely fibrillose or occasionally fibrillose-scaly, light violaceous brown to buff color, often with violaceous tints in young, fresh specimens ("Vinaceous-Buff," "Pale Vinaceous-Fawn," or "Pinkish Buff"); margin inrolled, decurved, plane or uplifted, entire, slightly undulate, eroded or rimose; context ≤ 9 mm thick at disc, tapering to margin, violaceous buff. **Lamellae** sinuate, arcuate or subdecurrent, close to distant, narrow to broad, thick, waxy-appearing, dark purple ("Dark Heliotrope Gray"

FIG. 46. Basidiomata of *L. amethysteo-occidentalis* (GMM 1256).

or "Deep Vinaceous-Gray"). **Stipe** (15–)45–190 × (2–)6–22(–36) mm, equal, subclavate, clavate or slightly bulbous, dry, coarsely fibrillose; fibrils forming longitudinal striations, recurved scales or both, at times forming reticulations at maturity; ground color concolorous with pileus; striations brownish to reddish brown. **Basal mycelium** scant to copious, violet. **Basidiospores** light violaceous or white in mass.

MICROMORPHOLOGY—**Pileipellis** of tightly interwoven hyphae with occasional widely scattered ± perpendicular individual hyphae, not fasciculate; terminal cells 24–66.5 × 4–10 μm, filamentous or barrel-shaped, olive brown in mass; walls up to 0.5 μm thick, olive brown; contents hyaline, light olive brown or light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown to olive brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–11.5 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 33–61 × 7–11.5 μm, clavate, hyaline; sterigmata (2–)4, up to 8 μm long. **Cheilocystidia** 23–63.5 × 2.3–8.9 μm, filamentous, subclavate or subcapitate, abundant, thin-walled, hyaline. **Basidiospores** (excluding ornamentation) [60/4] (6.4–)7–9.2(–11) × (6.4–)7–8.7(–9.7) μm ($\bar{x}$ = 7.9–8.4 × 7.4–8.1 μm), Q = (0.93–)1–1.13(–1.16) ($\bar{Q}$ = 1.02–1.06), globose to subglobose, hyaline, echinulate; echinulae 0.9–1.4(–2.3) μm long, 1–1.5 μm wide at base, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3.5–10.5 μm diam., tightly interwoven, filamentous, hyaline.

SOMATIC CULTURE MAT MORPHOLOGY (N = 3; Appendix B)—**PDA: Radius** at week 3 = 5–11 mm, week 6 = 7–23 mm; **mat** felty, thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, not translucent, at first bright violet, by week 6 violet coloration restricted to 2–3 mm band near margin, short aerial hyphae light grayish violet; **margin** 1–3 mm broad, thin, silky, becoming subfelty, even to uneven, light violet to white; **plug** often covered with white cottony hyphae, bright violet; **hyphae** morphologically undifferentiated, olivaceous brown in mass. **MMN: Radius** at week 3 = 11–19 mm, week 6 = 23–39 mm; **mat** silky,

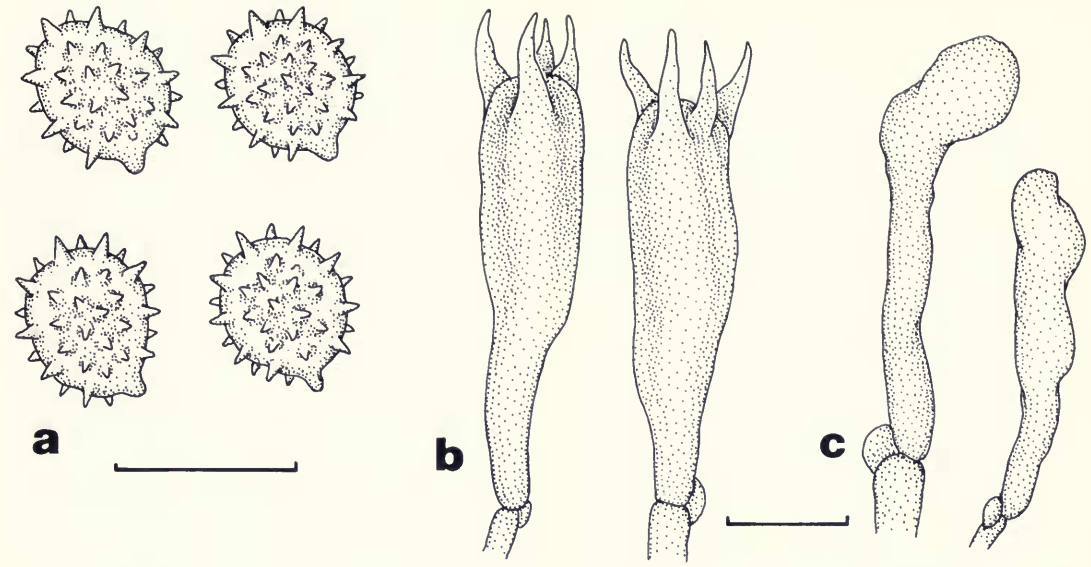


FIG. 47. Micromorphological features of *L. amethysteo-occidentalis* (E. Farwell 5015): **a,** basidiospores; **b,** basidia; **c,** cheilocystidia. Scale line = 10 μm.

subfelty or felty, thin to thick, interwoven, tightly appressed to agar surface, translucent, light violet, often with 1–3 concentric darker narrow bands; **margin** narrow, subfelty to silky, thin, entire to sulcate, light violet; **plug** concolorous with mat; **hyphae** morphologically undifferentiated. **MEA: Radius** at week 3 = 6–17 mm, week 6 = 10–33 mm; **mat** subfelty to felty, rarely silky, thin to thick, interwoven, tightly appressed to agar surface, translucent, white; **margin** not well differentiated, narrow, silky to subfelty, thin, even to undulate, white; **plug** white; **hyphae** morphologically undifferentiated.

HABITAT AND DISTRIBUTION—Solitary to scattered, rarely caespitose, commonly encountered in temperate deciduous forests of eastern North America, probably in association with *Quercus* and *Fagus*. Not reported from other continents. A list of specimens examined is provided in Appendix A.

OBSERVATIONS—*Laccaria ochropurpurea* can be distinguished easily from all other *Laccaria* taxa by its large size, light violaceous brown to buff colored pileus and stipe, dark purple, thick, waxy lamellae, and globose to subglobose basidiospores. The only North American species that could be confused with it are *L. nobilis* and faded collections of *L. amethysteo-occidentalis* and *L. trullissata*. These taxa all differ in basidiospore shape and size. In addition, *L. amethysteo-occidentalis* differs in having numerous, large cheilocystidia, and *L. nobilis* has reddish brown to orange-brown, strongly scaly basidiomata. Collections of *L. trullissata* have elongate, finely roughened basidiospores and are restricted to sand or sandy soil with sand covering much of their stipe and adhering to their basidiomata.

Culture mat morphology of the five isolates utilized showed the least intraspecific variation of all the taxa examined. The slow growth rate and dark purple color on PDA were distinctive (fig. 44).

Laccaria ochropurpurea appears to be restricted to deciduous–coniferous forests of eastern North America. Lahaie (1981) reported that it does not occur in the coniferous boreal forests of eastern Canada. Several reports of *L. ochropurpurea* occurring in western North America have been noted (personal communications and herbarium specimens), but all of the specimens investigated during this study appeared to be either *L. amethysteo-occidentalis* or *L. nobilis*.

Laccaria amethysteo-occidentalis G. M. Mueller. Figures 46, 47, 58a, 59d.

Laccaria amethysteo-occidentalis G. M. Mueller, Mycotaxon 20: 103–105. 1984. TYPE: Canada, British Columbia, near Squamish, Alice Lake Prov. Park campground, 3 October 1981, *G. M. Mueller 1256* (TENN 42526) (TENN!, holotype).

MACROMORPHOLOGY—**Pileus** 10–65(–89) mm broad, obtuse, convex or plane, often depressed,

not striate when fresh, occasionally becoming slightly translucent-striate upon fading, finely fibrillose, fibrillose, or fibrillose-scaly, hygrophanous, deep purple when fresh ("Taupe Brown," "Dull Indian Purple," "Dusky Dull Violet 1," "Dark Hyssop Violet," or "Slate-Violet"), fading to vinaceous ("Dark Vinaceous-Drab," "Dark Vinaceous-Gray," or near "Wood Brown"), finally buff color (near "Pale Ochraceous-Salmon"); margin inrolled, decurved, or plane, entire to eroded; context thin, concolorous with pileus ("Dark Slate-Violet") with lighter gray purple to white areas intermixed ("Pale Bluish Lavender"). **Lamellae** sinuate to arcuate, subdistant to distant, narrow to broad, thick, occasionally waxy appearing, dark violaceous ("Deep Slate Violet" to "Slate-Violet"), fading (near "Lavender"). **Stipe** 18–115 × 3–12 mm, equal, subclavate or slightly bulbose, dry, strongly longitudinally striate, occasionally with recurved scales, purple ("Dark Slate Purple," "Dark Vinaceous Brown," or "Hay's Brown"), often with lighter violet or white scattered sectors ("Pale Bluish Lavender"); context solid, concolorous with pileus context. **Basal mycelium** violet ("Dark Slate-Purple," "Deep Slate-Violet," or "Light Dull Bluish Violet"). **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of tightly interwoven hyphae with scattered fascicles of ± perpendicular hyphae, fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae 28–73.5 × 7–16 μm, filamentous, clavate or broadly clavate; walls up to 0.5 μm thick, vinaceous brown; contents hyaline to light vinaceous brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light vinaceous brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–11.5 μm diam., thin-walled, hyaline to light vinaceous brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 34–56 × 10–14.5 μm, clavate, hyaline, in young specimens vinaceous brown in mass; sterigmata 4, up to 9 μm long. **Cheilocystidia** 36.5–66.5 × 12–18.5 μm, subclavate to clavate, often abundant, thin-walled, hyaline. **Basidiospores** (excluding ornamentation) [81/6] 7.8–10.6 × 7–9.2 μm ($\bar{x}$ =9–9.8 × 7.4–8.6 μm), Q = (1–)1.06–1.24(–1.36) ($\bar{Q}$ = 1.13–1.19), subglobose to broadly ellipsoid, rarely globose or ellipsoid, echinulate; echinulae 0.5–1.4 (–1.8) μm long, ≤ 1 μm wide at base, crowded, hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2.5–8 μm diam., hyaline, morphologically undifferentiated.

SOMATIC CULTURE MAT MORPHOLOGY (N = 1; GMM 1256)—**PDA: Radius** at week 3 < 3 mm, week 6 = 12–14 mm; **mat** felty, thick, tightly interwoven, tightly appressed to agar surface, not translucent, dark violet; **margin** up to 3 mm broad, subfelty, abruptly thinner than mat, entire, light violet; **plug** dark violet; **hyphae** mostly morphologically undifferentiated, occasionally subcoralloid. **MMN: Radius** at week 3 = 14–22 mm, week 6 = 24–32 mm; **mat** felty, thick, tightly interwoven, thicker near plug, tightly appressed to agar surface, not translucent, moderate violet, darker near plug, lighter colored away from plug; **margin** 1–2 mm broad, subfelty to silky, not well differentiated from mat, even to serrate, light violet; **plug** moderate violet; **hyphae** same as in PDA. **MEA: Radius** at week 3 = 14–17 mm, week 6 = 23–27 mm; **mat** subfelty, thick, interwoven with a narrow (3 mm) thicker band at midpoint, tightly appressed to agar surface, translucent, white; **margin** 1–2 mm broad, subfelty, not well differentiated, entire to somewhat serrate, white; **plug** white; **hyphae** morphologically undifferentiated.

HABITAT AND DISTRIBUTION—Scattered to gregarious; under conifers (often *Pseudotsuga menziesii* (Mirb.) Franco) in western North America. A list of specimens examined is presented in Appendix A.

OBSERVATIONS—*Laccaria amethysteo-occidentalis* can be distinguished easily from the other two "purple" *Laccaria* taxa found in North America, *L. amethystina* and *L. vinaceobrunnea,* by its large size and deeper purple coloration of fresh basidiomata. Additionally, *L. amethysteo-occidentalis* differs from *L. amethystina* in having nonglobose, more finely echinulate basidiospores and from *L. vinaceobrunnea* in the arrangement of the hyphae composing the pileipellis. All three taxa have large cheilocystidia that form a substerile layer along the lamellar margin. This character can be used in many cases to separate herbarium material of *L. amethysteo-occidentalis* from *L. nobilis.*

Homokaryotic isolates of this taxon were intersterile with isolates of other tested taxa, including *L. amethystina* and *L. vinaceobrunnea.*

The above description of culture mat morphology was based on a single isolate, even though numerous attempts were made to culture from basidiomata of this species. The slow rate of growth and dark purple color of the culture mat on PDA were similar to that exhibited by cultures of *L. ochropurpurea.*

Laccaria amethysteo-occidentalis can be found

commonly in the coniferous forests of northwestern United States and western Canada. In contrast, *L. amethystina* appears to be restricted to the temperate deciduous or mixed coniferous–deciduous forests in eastern North America and Europe and the tropical *Quercus* forests of Central America and Colombia.

Laccaria amethystina Cooke. Figures 48, 49, 58b, 60a.

≡ *Agaricus amethystinus* Hudson, Fl. angl. 2: 612. 1778; *non Agaricus amethystinus* Scopoli, Fl. carn. 2: 437. 1772 [= *Cortinarius* sp.]; *nec Agaricus amethystinus* Schaeffer, Fung. Bavar. Palat. nasc. 4: 24. 1774 [= *Cortinarius traganus*]. TYPE: England, Devon, Dartmoor, Two Bridges, Whistmans Wood, 6 September 1971, *D. N. Pegler s.n.* (as *L. amethystea*) (K!, neotype *fide* Mueller & Vellinga, 1990).

≡ *Laccaria amethystina* Cooke, Grevillea 12: 70. 1884.

≡ *Collybia amethystina* (Cooke) Quélet, Fl. mycol. France: 237. 1888.

≡ *Clitocybe amethystina* (Cooke) Peck, Annual Rep. New York State Bot. 50: 128. 1897.

= *Agaricus amethysteus* Bulliard, Herb. France: pl. 198. 1784. [= *A. laccatus* Schaeff., Fung. Bavar. Palat. nasc. 4: 8. 1774].

≡ *Omphalia amethystea* (Bulliard) S. F. Gray, Nat. Arr. Brit. Pl. 1: 614. 1821.

≡ *Agaricus laccatus* var. *amethysteus* (Bulliard) Berkeley & Broome, J. Linn. Soc., Bot. 11: 518. 1871.

≡ *Russuliopsis laccata* var. *amethystea* (Bulliard) J. Schroeter *in* Cohn, Krypt.-Fl. Schlesien 3(1): 623. 1889. [erroneously written '*amethystina*'].

≡ *Laccaria amethystea* (Bulliard) Murrill, N. Amer. Fl. 10: 1. 1914.

= *Laccaria calospora* Singer, Beih. Sydowia 7: 7. 1973.

MACROMORPHOLOGY—**Pileus** 5–32(–53) mm broad, convex to plane, often depressed, not striate or striate, occasionally translucent-striate when fresh, finely pruinose to fibrillose, occasionally becoming finely fibrillose-scaly, strongly hygrophanous, bright grayish purple when fresh (near "Heliotrope-Slate" or "Dark Slate-Violet 1"), fading to buff ("Vinaceous-Gray," "Pale Ochraceous-Buff," or "Light Buff"); margin inrolled to decurved, entire to undulate, occasionally eroded; context up to 3 mm thick at disc, tapering to margin, concolorous with surface. **Lamellae** sinuate to arcuate, subdistant to distant, up to 5 mm broad, thick, subconcolorous with pileus ("Heliotrope-Slate" or "Vinaceous-Drab"). **Stipe** 6–58(–70) × 1–7 mm, equal, subclavate or slightly bulbous, dry, fibrillose, longitudinally striate, concolorous with pileus. **Basal mycelium** hygrophanous, violet becoming white. **Basidiospores** white or very pale violet in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae or with scattered individual ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of perpendicular hyphae 23–73.5 × 6.5–17 μm, filamentous, clavate, broadly clavate, capitate or ventricose-rostrate, walls up to 0.5 μm thick, vinaceous brown in young specimens, light yellowish brown in mature specimens; contents concolorous with hyphal walls. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown or vinaceous brown. **Lamellar trama** parallel to subparallel; hyphae mostly 3.5–16 μm diam., thin-walled hyaline to light yellowish brown or vinaceous brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 30–64.5 × 8.5–14 μm, clavate, hyaline; sterigmata (2–)4, up to 10 μm long. **Cheilocystidia** 25.5–64(–92) × 4–12 μm, filamentous, clavate, broadly clavate or ventricose-rostrate, abundant, thin-walled hyaline. **Basidiospores** (excluding ornamentation) [160/11] 7–10 (–10.6) × (6.4–)7–10(–10.6) μm ($\bar{x}$ = 7.7–9 × 7.7–9 μm), Q = 1–1.07(–1.12) ($\bar{Q}$ = 1–1.02), globose, rarely subglobose, hyaline, echinulate; echinulae 1.4–2.8 μm long, > 1.2 μm wide at base; hilar appendix 1.3–2 μm, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–12 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

HABITAT AND DISTRIBUTION—Solitary to scattered, occasionally caespitose; associated with *Quercus* and *Fagus* in temperate deciduous or mixed deciduous–coniferous forests of eastern North America and Europe, under species of *Quercus* in Central America and northern South America.

OBSERVATIONS—*Laccaria amethystina* can be distinguished from the other North American "purple" *Laccaria* (*L. amethysteo-occidentalis* and *L. vinaceobrunnea*) by its small size and stature, bright grayish purple basidiomata that fade directly to buff, and globose, coarsely echinulate basidiospores.

No tissue cultures of *L. amethystina* were obtained during this study. Homokaryotic and reconstituted dikaryotic isolates were violet on MMN and PDA and grew moderately fast (radius at week 6 = ± 50 mm).

Homokaryotic isolates of *L. amethystina* were intersterile with isolates of other taxa, including

FIG. 48. Basidiomata of *L. amethystina* (GMM 1718).

L. amethysteo-occidentalis and *L. vinaceobrunnea*. One North American isolate and one Swedish isolate of *L. amethystina* were included in RFLP analyses (Gardes et al., 1990, 1991a). These two isolates had different RFLP patterns, indicating that genetic divergence may have occurred between North American and Swedish populations of *L. amethystina*. However, the amount of intrapopulation variation is not known because only one isolate was examined from each population.

Mueller and Vellinga (1986, 1990) discussed the controversy that has persisted in the literature as to the correct name for this taxon. Most workers use the name *L. amethystina*; however, Murrill (1914), Dennis et al. (1960), and others have used *L. amethystea* (Bulliard) Murrill for this species. Cooke's name is the earliest valid name for the taxon.

Laccaria gomezii Singer & G. M. Mueller (Mueller & Singer, 1988) grows sympatrically with *L. amethystina* in Costa Rica and Colombia. Collections of *L. gomezii* are characterized by having purple basidiomata that quickly turn vinaceous brown and then brown; adnate to decurrent, close to crowded, thin lamellae; and subglobose to ellipsoid basidiospores.

Laccaria amethystina appears to be restricted to temperate deciduous or mixed coniferous–deciduous forests in eastern North America and Europe and to Neotropical *Quercus* forests in Central America and Colombia. Lahaie (1981) did not report material of *L. amethystina* from boreal coniferous forests in Canada. Mueller (1991a) reported collections of this taxon from southern Sweden.

Laccaria vinaceobrunnea G. M. Mueller. Figures 50–52, 58c, 73c.

Laccaria vinaceobrunnea G. M. Mueller, Mycotaxon 20: 114–115. 1984. TYPE: USA, Louisiana, Tammany Parish, Fountainbleu State Park, under *Quercus virginiana*, 9 December 1980, *G. M. Mueller 1120* (TENN 42525) (TENN!, holotype).

MACROMORPHOLOGY—**Pileus** 7–25(–42) mm broad, obtuse to convex, becoming plane to up-

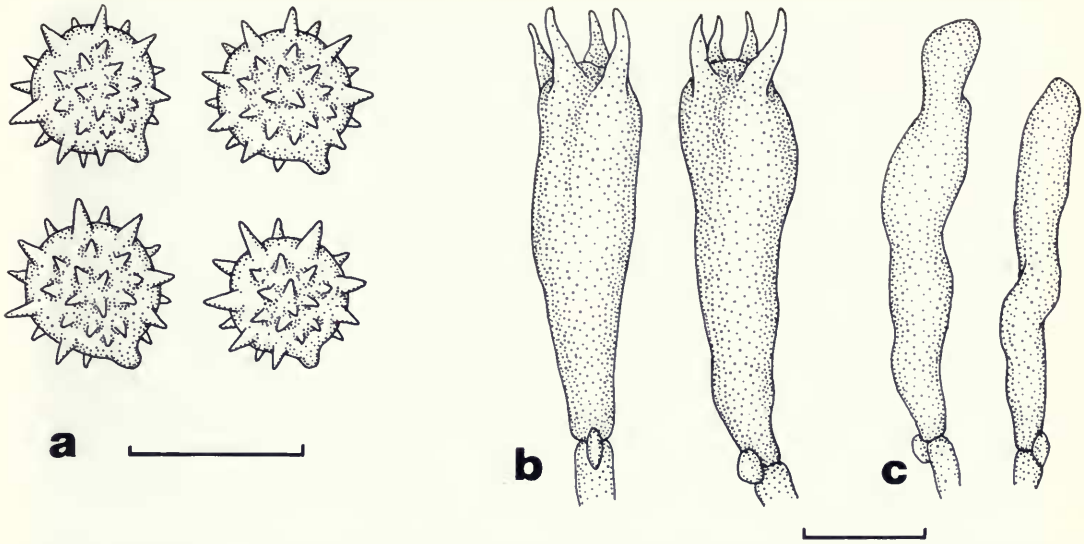


FIG. 49. Micromorphological features of *L. amethystina* (GMM 2237): **a**, basidiospores; **b**, basidia; **c**, cheilocystidia. Scale line = 10 μm.

lifted, often depressed, not striate or finely striate when wet, finely fibrillose, occasionally finely fibrillose-scaly, hygrophanous, when immature violaceous (near "Purplish Lilac"), becoming vinaceous (Dark Vinaceous-Brown," "Hay's Brown," or "Vinaceous-Brown"), reddish brown ("Cameo Brown" to "Walnut Brown") then fading to orange-brown or buff ("Cinnamon-Rufous" to "Light Ochraceous-Buff"); margin decurved to plane, entire to eroded; context thin, tapering to margin, light vinaceous ("Light Brownish Vinaceous" to near "Vinaceous-Fawn"). **Lamellae** adnate to arcuate, subdistant to distant, broad, thick, waxy, purple ("Purplish Lilac" or "Purplish Vinaceous"). **Stipe** 7–56(–98) × 2–7 mm, equal, subclavate or slightly bulbous, dry, fibrillose, occasionally with recurved fibrils or finely striate, concolorous with pileus; fibrils ("Hazel" or "Vinaceous-Brown"). **Basal mycelium** violet. **Basidiospores** white in mass.

MICROMORPHOLOGY—**Pileipellis** of interwoven hyphae with very numerous ± perpendicular hyphae; terminal cells 32–78 × 7–14.5 μm, filamentous to clavate, hyaline to light vinaceous; walls up to 0.5 μm thick; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline to light olive brown in mass. **Lamellar trama** parallel; hyphae thin-walled, hyaline; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 33–60 × 8.5–9 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Cheilocystidia** 31.5–92 × 5.5–11 μm, filamentous to clavate, abundant, hyaline. **Basidiospores** (excluding ornamentation) [60/4] (7–)7.4–10(–10.6) × 6.4–9.2(–9.7) ($\bar{x}$ = 8.2–8.9 × 7.3–8.3 μm), Q = 1–1.26 ($\bar{Q}$ = 1.07–1.15), subglobose to broadly ellipsoid, occasionally globose, hyaline, echinulate; echinulae 0.5–1.8 μm long, ≤ 1 μm wide at base; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–8 mm diam., filamentous, tightly interwoven, hyaline.

HABITAT AND DISTRIBUTION—Scattered to gregarious, often caespitose. Growing in sandy soil under *Quercus virginiana* Miller along the Gulf Coast. A list of specimens examined is provided in Appendix A.

OBSERVATIONS—*Laccaria vinaceobrunnea* can be distinguished from *L. amethystina* and *L. amethysteo-occidentalis* by habitat, coloration, unique pileipellis, and subglobose to broadly ellipsoid basidiospores. The abundant, large cheilocystidia is a reliable character to use in identifying herbarium collections that lack notes on macromorphology.

Homokaryotic isolates of *L. vinaceobrunnea* were intersterile with tested isolates of other taxa, including *L. amethystina* and *L. amethysteo-occidentalis*.

Material referable to this taxon has not been reported from outside of the Gulf Coast area. Although not yet reported, I would expect it to be found in northeastern Mexico.

FIG. 50. Basidiomata of *L. vinaceobrunnea* (GMM 1120).

FIG. 51. Basidiomata of *L. vinaceobrunnea* (GMM 2337).

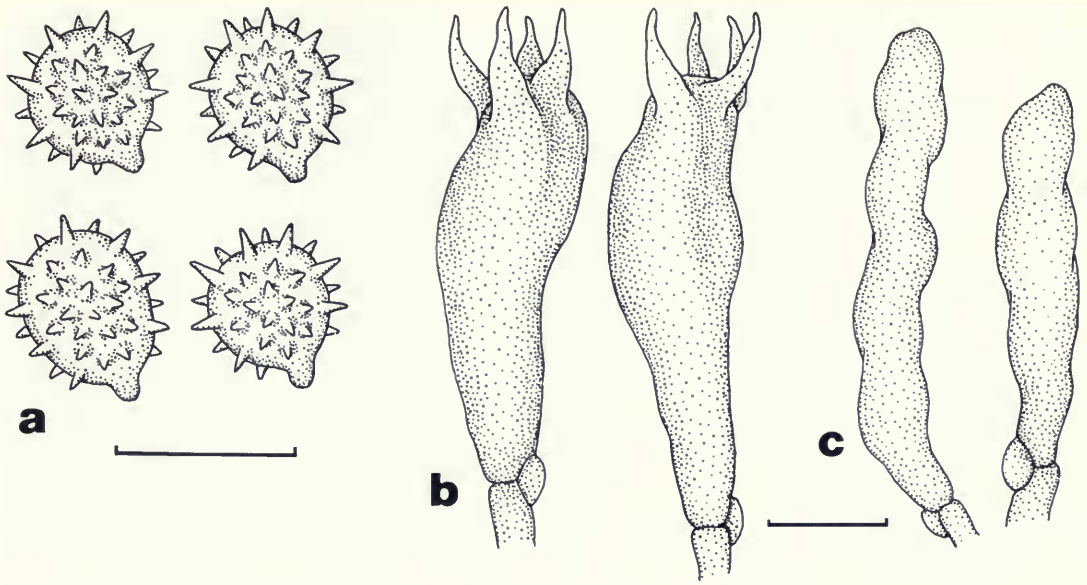


FIG. 52. Micromorphological features of *L. vinaceobrunnea* (GMM 2335): **a,** basidiospores; **b,** basidia; **c,** cheilocystidia. Scale line = 10 μm.

Tentative Key to *Laccaria* for the World

The concepts for extralimital taxa included in the following key are based on an examination of type specimens and descriptions and a review of the literature. Only those taxa that I tentatively recognize are treated. The key is presented for two reasons: (1) to summarize the delimiting characters of the taxa involved and (2) to provide a framework that will facilitate further taxonomic work on the genus. It is not presented as a definitive statement on the genus for the world.

1. Lamellae gray; Japan 2
1. Lamellae violaceous, purple, flesh color or pink when fresh 3
   2. Basidia bisporic; basidiospores 8–11 μm diam., globose, echinulae 2–3 μm long; pileus grayish, almost black ..... *L. nigra* Hongo (p. 111)
   2. Basidia tetrasporic; basidiospores 7.5–10 μm diam., globose, verruculose; pileus becoming mouse gray or subavellaneous ..... *L. murina* Imai (p. 111)
3. Lamellae violaceous to purple when young and fresh 4
3. Lamellae flesh color to pinkish when fresh 18
   4. Basidiospores large, 13.5–22 × 5.5–9.5 μm, elongate, smooth to finely roughened or finely echinulate (echinulae < 0.5 μm long); in sand or very sandy soil 5
   4. Basidiospores smaller (< 10.5 μm long), less elongate ($\bar{Q} \leq 1.51$), echinulae > 0.5 μm long; in sand or not in sand 6
5. Basidiospores elongate ($\bar{Q} = 2.37$–2.51), finely roughened, not echinulate; eastern North America ..... *L. trullissata* (Ellis) Peck (p. 131)
5. Basidiospores less elongate ($\bar{Q} = 1.67$–1.81); echinulae 0.2–0.5 μm long; northern Europe, rare in eastern North America ..... *L. maritima* (Teod.) Singer *ex* Huhtinen (p. 107)
   6. Lamellae bright violaceous or purple 7
   6. Lamellae pallid violaceous to vinaceous when young, fading to vinaceous flesh color 13
7. Pileus bright violaceous, purple or grayish black when young and fresh 8
7. Pileus fawn or buff color, often with violaceous tints 12
   8. Pileus fuscous black; lamellae purple to grayish lavender; stipe apex purple, base vinaceous brown;

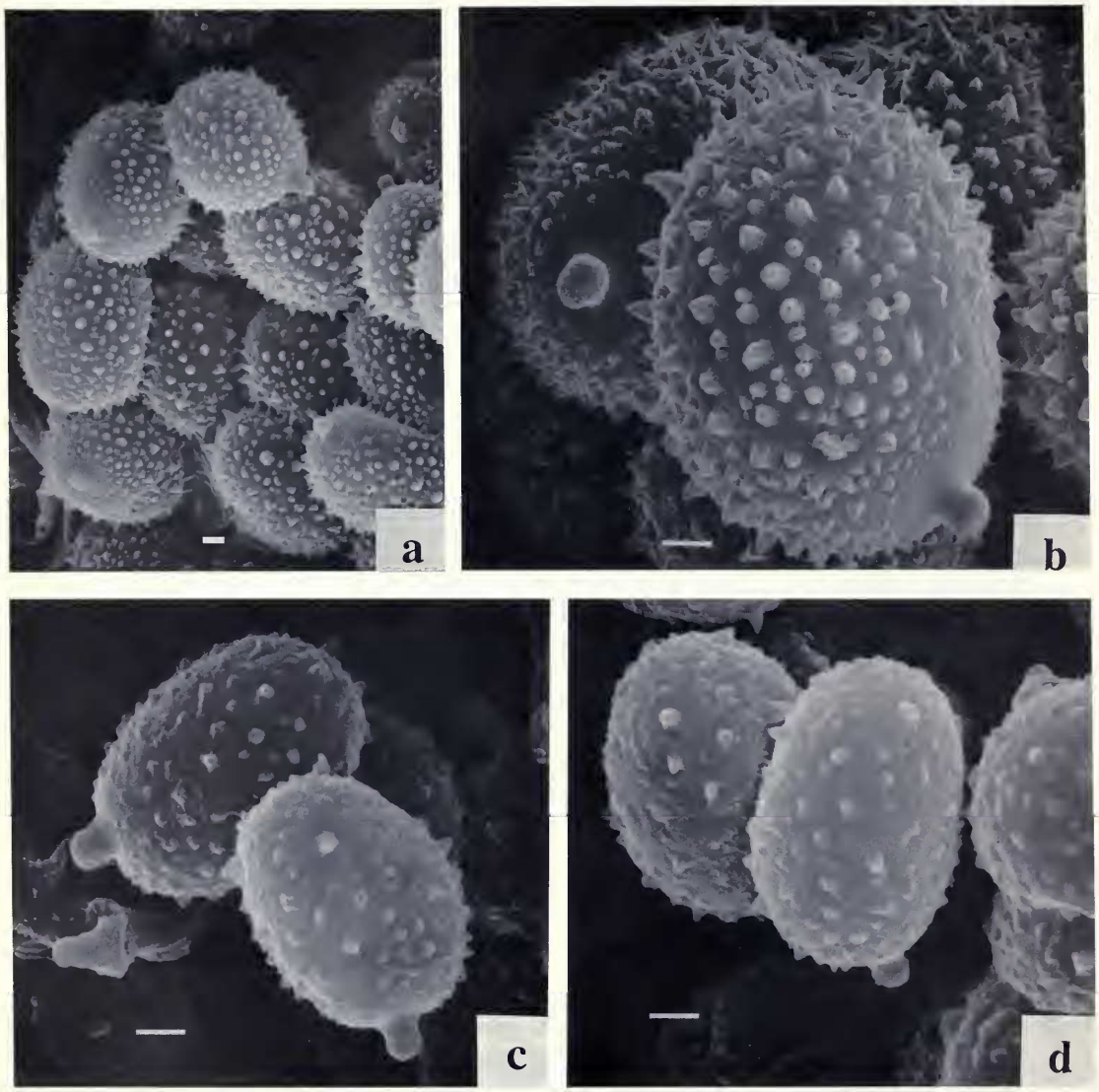


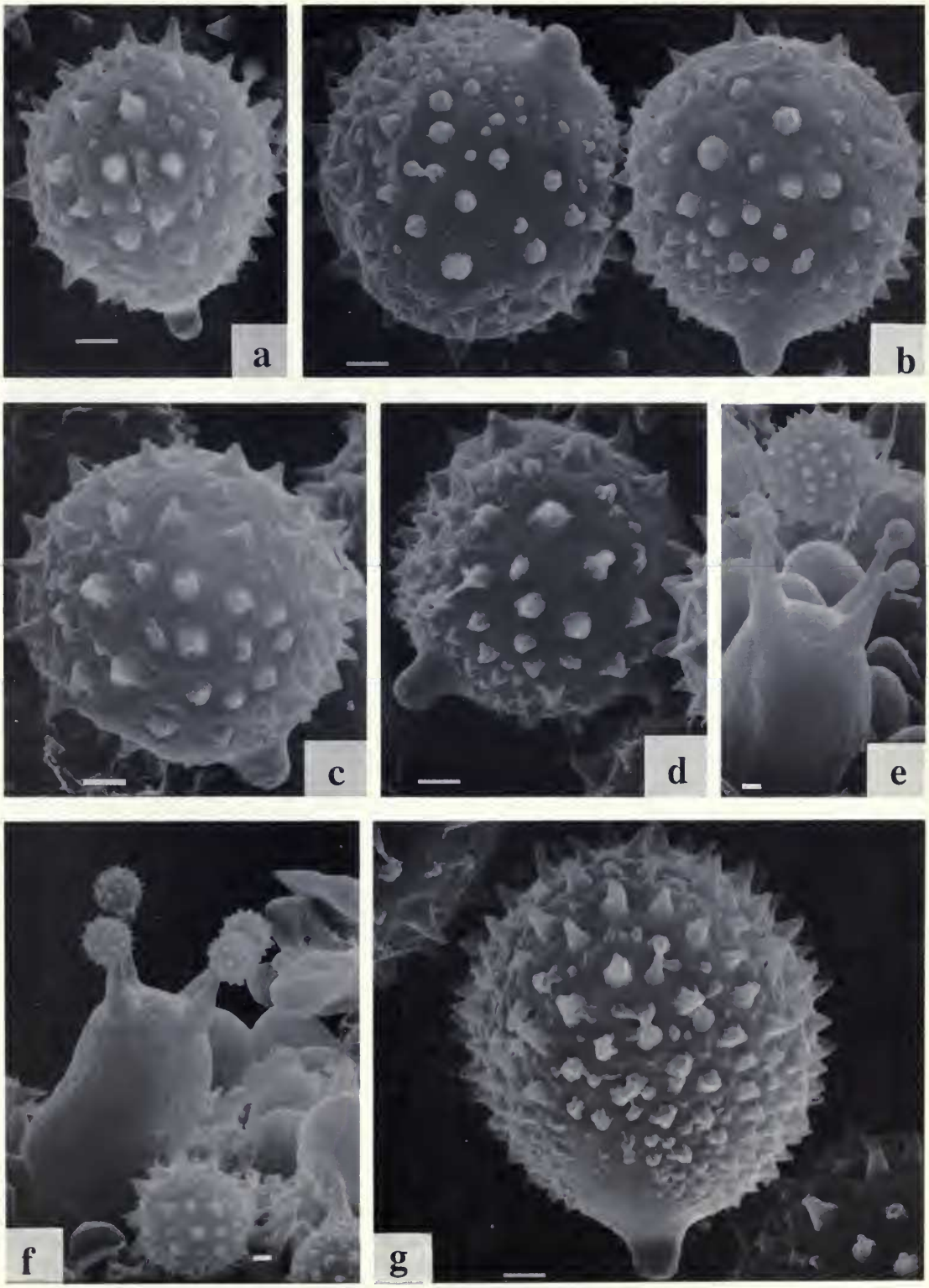
FIG. 53. SEMs of basidiospores: **a, b,** *L. proxima* (GMM 2100); **c, d,** *L. oblongospora* (GMM 2310). Note differences in basidiospore size and shape. Scale lines = 1 μm.

cheilocystidia 30–40 × 2–6.5 μm, filamentous, numerous; New Zealand ..... *L. violaceoniger* Stevenson (p. 133)

8. Basidiomata and lamellae bright violaceous or purple when young and fresh; cheilocystidia larger (up to 92 × 12 μm) clavate, numerous 9
9. Basidiospores globose; echinulae > 1 μm wide at base; basidiomata fading from amethyst to grayish to buff ..... *L. amethystina* Cooke (p. 86)

→

FIG. 54. SEMs of basidiospores: **a,** *L. longipes* (A. Parker *s.n.*); **b,** *L. fraterna* (GMM 2126); **c,** *L. montana* (GMM 1813); **d–f,** *L. laccata* var. *pallidifolia* (GMM 1845); **g,** *L. pumila* (GMM 1956). Note differences in basidiospore size and shape. Scale lines = 1 μm.


a
b
c
d
e
f
g

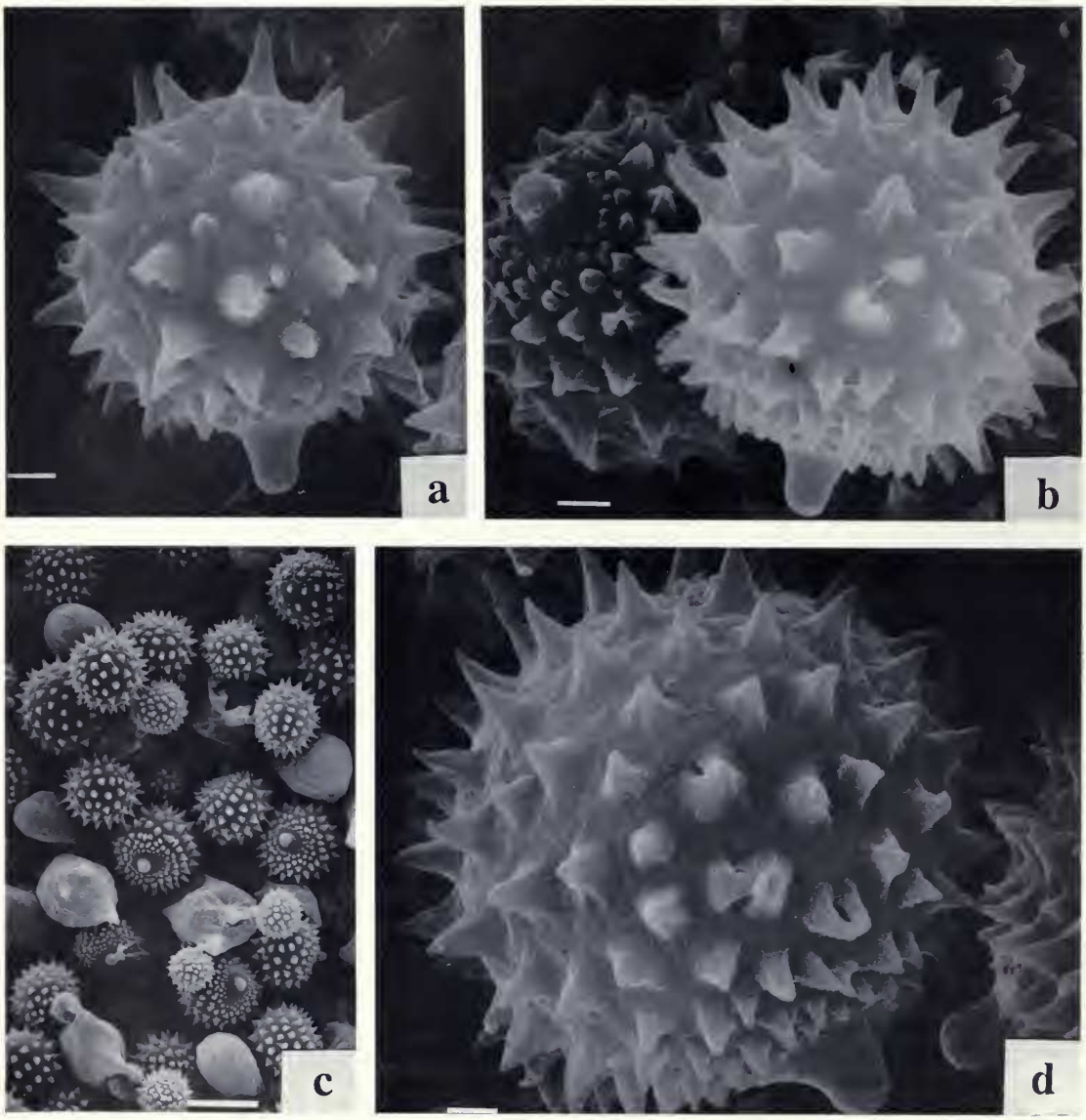


FIG. 55. SEMs of basidiospores: **a,** *L. ohiensis* (GMM 2354); **b,** *L. striatula* (GMM 1944); **c–d,** *L. tortilis* (McAdoo 78#28). Note the long and wide echinulae on all basidiospores. Scale lines for a, b, & d = 1 μm. Scale line for c = 10 μm.

9. Basidiospores subglobose to broadly ellipsoid; echinulae < 1 μm wide at base; basidiomata fading from amethyst to brown to buff 10
   10. Basidiomata large (pileus 10–90 mm diam.), amethyst becoming vinaceous; pileipellis hyphae interwoven with scattered fascicles of perpendicular hyphae; western North America; under conifers ..... *L. amethysteo-occidentalis* G. M. Mueller (p. 86)
   10. Basidiomata smaller (pileus 7–38[–65] mm diam.); amethyst to dark reddish purple, becoming reddish brown or vinaceous brown at maturity; associated with subtropical or tropical species of *Quercus* 11
11. Basidiomata violaceous, becoming vinaceous brown then reddish brown; lamellae adnate to arcuate,

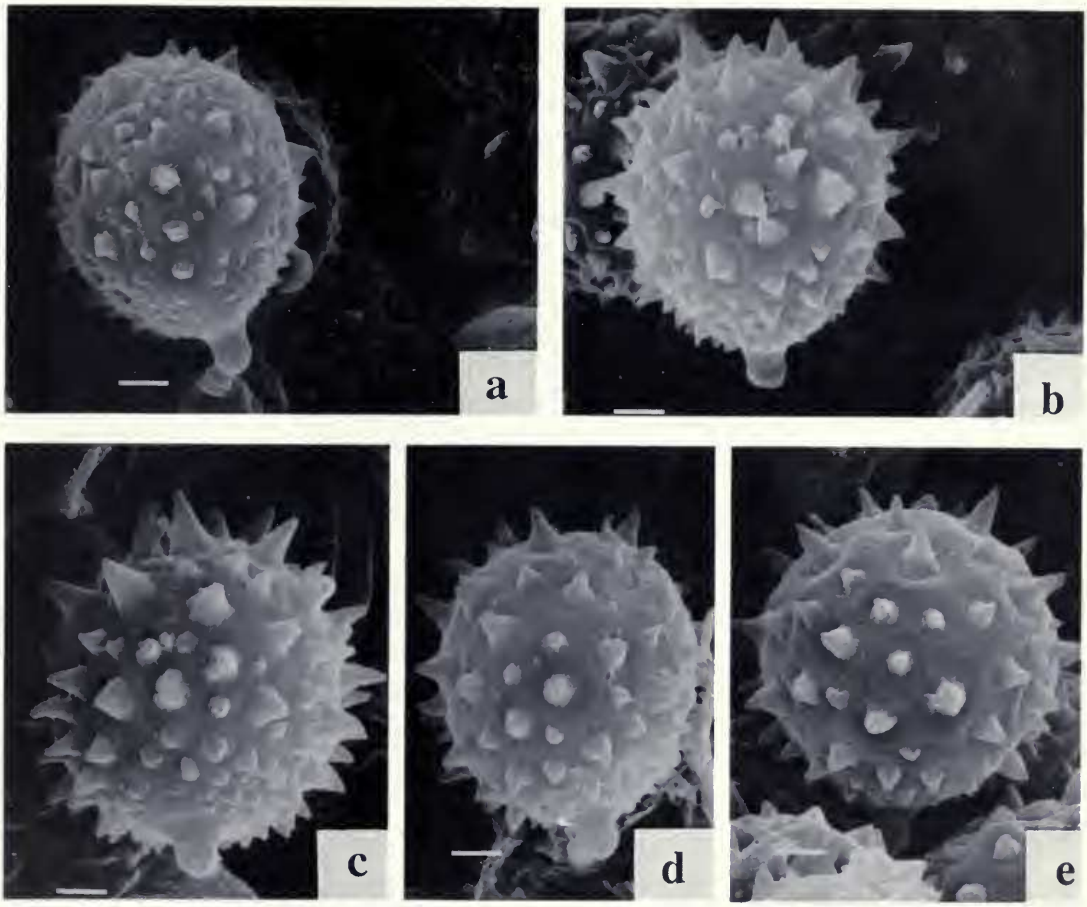


FIG. 56. SEMs of basidiospores: **a**, *L. bicolor* (GMM 2027); **b**, *L. bicolor* (GMM 2038); **c**, *L. trichodermophora* (GMM 2306); **d**, **e**, *L. nobilis* (GMM 2048). Note relatively small basidiospore size. Scale line = 1 μm.

subdistant to distant; pileipellis hyphae interwoven with numerous large, individual, perpendicular hyphae; North America, Gulf Coast states ..... *L. vinaceobrunnea* G. M. Mueller (p. 133)

11. Basidiomata dark violet purple to dark reddish purple, becoming vinaceous brown; lamellae adnate to subdecurrent, crowded to close, thin; Costa Rica and Colombia ..... *L. gomezii* Singer & G. M. Mueller (p. 99)
    12. Lamellae dark purple, thick, waxy appearing; basidiomata large (pileus up to 60–120 mm diam.), violaceous buff when young and fresh, becoming buff; eastern North America ..... *L. ochropurpurea* (Berk.) Peck (p. 114)
    12. Lamellae lilac; basidiomata smaller, pileus fawn-colored with fulvous fibrils; New Zealand .. .. *L. lilacina* Stevenson (p. 105)
13. Pileus dark purple-brown, fading to light purple-brown; stipes purplish brown at base; western Europe ..... *L. purpureobadia* Reid (p. 123)
13. Pileus orange-brown, pinkish flesh color, reddish brown, light violaceous, or buff color; stipe ± concolorous 14
    14. Pileus strongly radially fibrillose, buff with vinaceous tints; fibrils dark brown to black; margin often dentate to lacerate; New Zealand ..... *L. fibrillosa* McNabb (p. 95)
    14. Pileus not radially fibrillose, pinkish flesh color to reddish brown; margin entire to slightly undulate 15

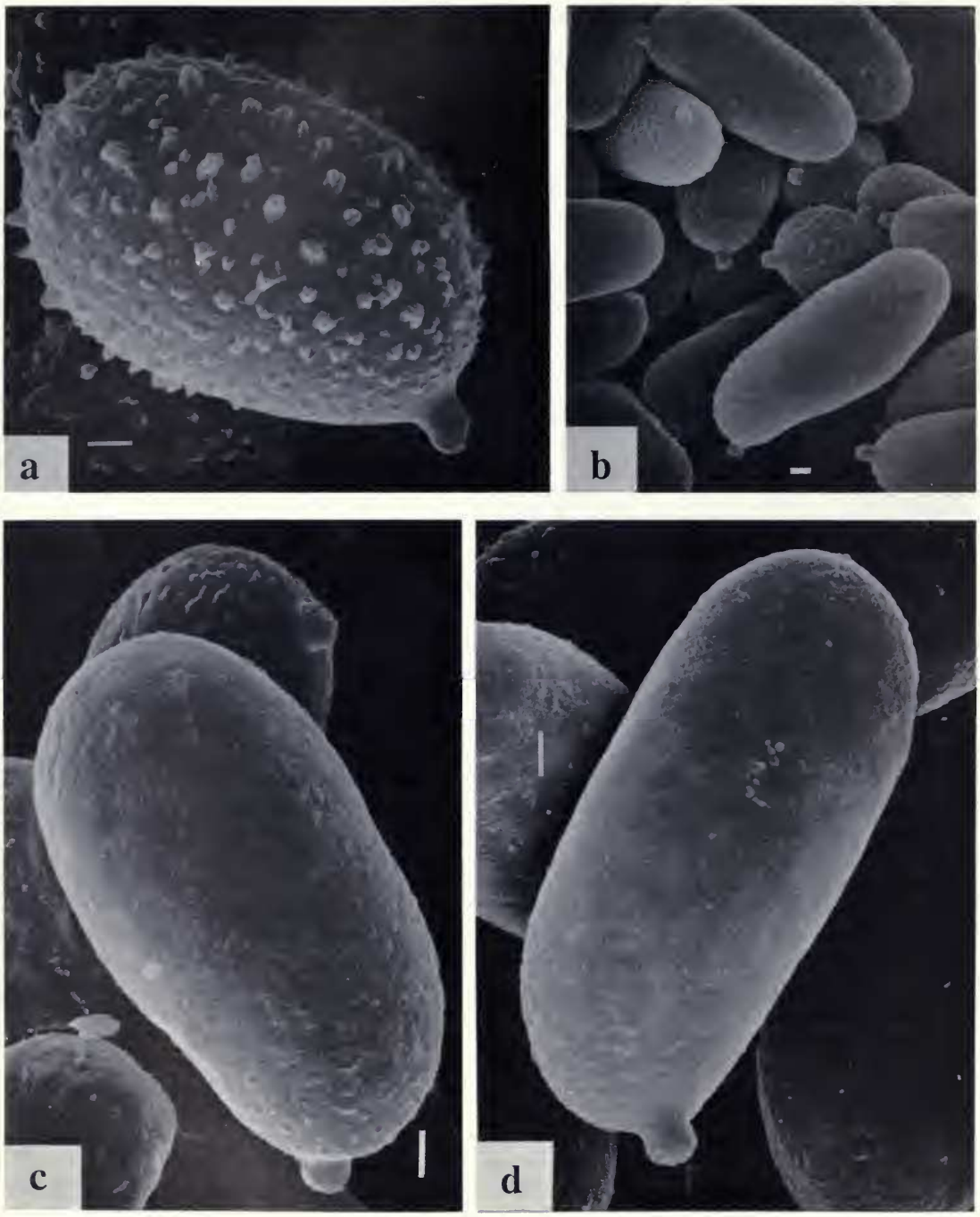


FIG. 57. SEMs of basidiospores: **a**, *L. maritima* (DAOM 159709); **b–d**, *L. trullissata* (GMM 1914). Note the differences in ornamentation and basidiospore shape. Scale line = 1 μm.

15. Basidiomata violet when young, fading buff with only traces of violet remaining; basidiospores globose; New Zealand 16
15. Basidiomata orange-brown, pinkish flesh color or reddish brown; basidiospores subglobose to subellipsoid; North America and Europe 17

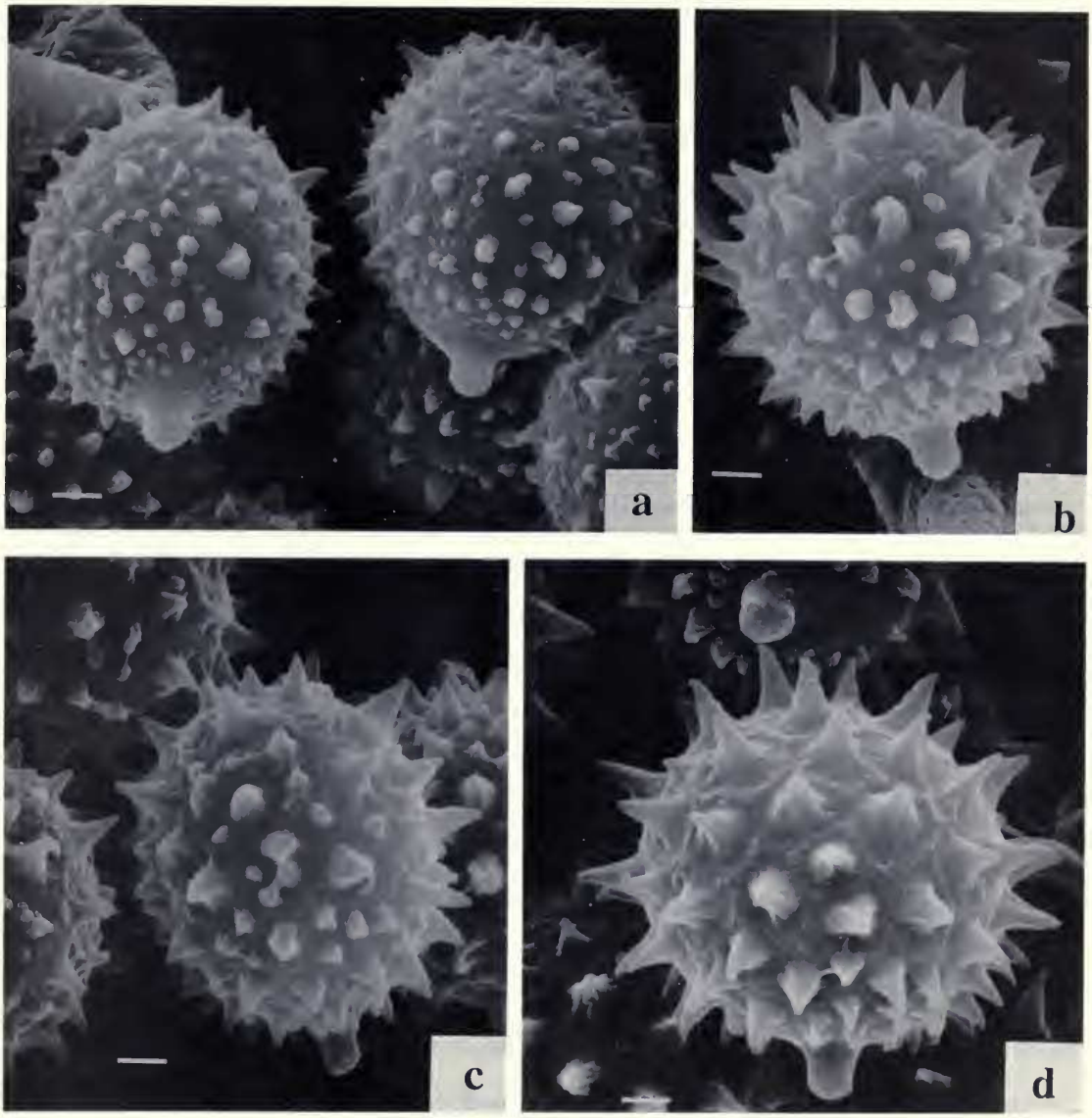


FIG. 58. SEMs of basidiospores: **a,** *L. amethysteo-occidentalis* (E. Farwell 5015); **b,** *L. amethystina* (GMM 2237); **c,** *L. vinaceobrunnea* (GMM 2335); **d,** *L. ochropurpurea* (E. Farwell 5074). Note differences in basidiospore shape and echinulae length and width. Scale line = 1 μm.

16. Basidiospore ornamentation < 2 μm long .... *L. masonii* var. *brevispinosa* McNabb (p. 89)
16. Basidiospore ornamentation > 2 μm long ..... *L. masonii* var. *masonii* Stevenson (p. 107)
17. Pileus 16–85 mm diam., often strongly scaly to squarrose; stipe large and robust (26–110[–160] × 4–10[–16] mm), strongly striate to reticulate; western North America and upper Great Lakes region ..... *L. nobilis* G. M. Mueller (p. 113)
17. Pileus 8–50(–70) mm, finely fibrillose to minutely scaly; stipe smaller ([23–]30–85[–130] × 3–6 [–10] mm), not strongly striate; western North America, upper Great Lakes region and Europe .. .. *L. bicolor* (Maire) Orton (p. 88)
18. Basidia (3)4-sterigmate 19

18. Basidia 2(3)-sterigmate 36
19. Basidiospores broadly ellipsoid to oblong ($\bar{Q}$ = 1.24–1.6); echinulae < 1 μm long 20
19. Basidiospores globose to ellipsoid; echinulae > 1 μm long 22
20. Basidiospores $\bar{x}$ = 8.3–9 × 5.6–6 μm, oblong ($\bar{Q}$ = 1.45–1.6); mycelium at stipe base violet, fading to white; Gulf Coast states ..... *L. oblongospora* G. M. Mueller (p. 113)
20. Basidiospores $\bar{x}$ = 9–11.5 × 6.7–8(–8.8) μm, ellipsoid ($\bar{Q}$ = 1.24–1.34[–1.43]); mycelium at stipe base white 21
21. Stipe context flesh color, lacking purple stains at base of stipe; widely distributed ..... *L. proxima* (Boud.) Pat. (p. 119)
21. Stipe context purple toward base, often with purple stains at stipe base; southern Argentina and Chile ..... *L. proximella* Singer (p. 120)
22. Mycelium at stipe base violaceous when fresh, becoming white with age; basidiospores small ($\bar{x}$ = 7–8.3[–9] × 6–8 μm) 23
22. Mycelium at stipe base white from onset; basidiospores larger ($\bar{x}$ = 8.2–13 μm long) (but see no. 32, *L. longipes*) 26
23. Lamellae flesh color to pinkish flesh color; basal mycelium usually scant, hygrophanous; basidiomata orange-brown; pileipellis a trichodermium or of interwoven hyphae with numerous large fascicles of perpendicular hyphae; southeastern United States, Mexico, Central America 24
23. Lamellae light vinaceous, occasionally fading to pinkish color; basal mycelium copious; basidiomata pinkish flesh color to reddish brown; pileipellis hyphae interwoven with scattered fascicles of perpendicular hyphae; western and central North America and Europe 25
24. Cheilocystidia small, filamentous, present or absent; southeastern North America, Mexico, Central America ..... *L. trichodermophora* G. M. Mueller (p. 130)
24. Cheilocystidia large and vesiculose (up to 9.5 μm diam.); Mexico ..... *L. bullulifera* Singer (p. 90)
25. Pileus 16–85 mm diam., often strongly scaly to squarrose; stipe large and robust (26–110[–160] × 4–10[–16] mm), strongly striate to reticulate; western North America and upper Great Lakes region ..... *L. nobilis* G. M. Mueller (p. 113)
25. Pileus 8–50(–70) mm, finely fibrillose to minutely scaly; stipe smaller ([23–]30–85[–130] × 3–6 [–10] mm), not strongly striate; western North America, upper Great Lakes region and Europe ..... *L. bicolor* (Maire) Orton (p. 88)
26. Pileus dark ochraceous brown, with light blue pruinae; USSR ..... *L. chibinensis* Michal. (p. 92)
26. Pileus orange-brown, pinkish flesh color or vinaceous brown 27
27. Basidiospores relatively large ($\bar{x}$ = 9.4–12.6 × 8.5–10.5 μm); pileus striate; restricted to arctic, boreal, or alpine habitats ..... *L. montana* Singer (p. 110)
27. Basidiospores smaller ($\bar{x} \leq$ 9[–10] μm long); pileus not striate, finely striate or translucent-striate 28
28. Basidiospores globose; echinulae > 1.5 μm long and ≥ 1.2 μm wide at base 29
28. Basidiospores globose to ellipsoid; echinulae ≤ 1 μm wide at base 31
29. Stipe 12–25(–40) × 1–2 mm, concolorous with pileus; among mosses or not; eastern North America, Central and South America, Europe ..... *L. ohiensis* (Mont.) Singer (p. 115)
29. Stipe 20–70(–103) × 1–4 mm, darker than pileus; in moist areas, often among mosses (not *Sphagnum*); eastern North America or New Zealand 30
30. Occurring in eastern North America ..... *L. striatula* (Peck) Peck (p. 126)
30. Occurring in New Zealand ..... *L. glabripes* McNabb (p. 99)
31. Pileus strongly translucent-striate; stipe 60–138(–165) mm long; growing among mosses, especially *Sphagnum,* usually in bogs 32
31. Pileus not striate or striate, not strongly translucent-striate; stipe ≤ 65(–106) mm long; growing among mosses or not, not normally found in bogs; widely distributed 34
32. Basidiospores $\bar{x}$ = 7.6–7.8 × 6.8–7.2 μm; North America ..... *L. longipes* G. M. Mueller (p. 106)
32. Basidiospores $\bar{x}$ = 8–10 μm long 33
33. Basidiospores subglobose to broadly ellipsoid; Europe .... *L. laccata* var. *moelleri* Singer (p. 108)

33. Basidiospores ellipsoid; south temperate forests of South America, Tierra del Fuego to Valdivian forests of Chile; under *Nothofagus* ..... *L. galerinoides* Singer (p. 97)
    34. Basidiospores broadly ellipsoid to ellipsoid ($\bar{Q}$ = 1.2–1.3); rarely encountered ..... *L. laccata* (Scop.: Fr.) Cooke var. *laccata* (p. 103)
    34. Basidiospores globose to very broadly ellipsoid ($\bar{Q}$ usually < 1.15) 35
35. Pilei brownish vinaceous; Japan ..... *L. vinaceoavellanea* Hongo (p. 131)
35. Pilei orange-brown to flesh color; common; North America and Europe ..... *L. laccata* var. *pallidifolia* (Peck) Peck (p. 116)
    36. Basidiospores < 11 μm diam. 37
    36. Basidiospores most > 11 μm diam. 40
37. Pileus not striate, reddish tawny or rose tawny; under native European trees ..... *L. impolita* Vellinga & G. M. Mueller (p. 102)
37. Pileus striate, rusty red or light brown; under *Eucalyptus* and other Australasian trees 38
    38. Basidiomata light brown ..... *L. canaliculata* (Cooke & Massee) Pegler (p. 92)
    38. Basidiomata rusty red; lamellae pink 39
39. Pleurocystidia absent; widely distributed ..... *L. fraterna* (Cooke & Massee) Pegler (p. 96)
39. Pleurocystidia present; New Zealand ..... *L. ohiensis* var. *paraphysata* McNabb (p. 117)
    40. Basidiospores 11–17 × 10–14.5 μm, subglobose to broadly ellipsoid ($\bar{Q}$ = 1.1–1.19); echinulae < 1.5 μm long; montane, boreal, or arctic habitats ..... *L. pumila* Fayod (p. 121)
    40. Basidiospores 10–15 × 10–15 μm, globose, echinulae > 2 μm long 41
41. Pileus striate, strongly undulate to distorted, orange-brown; North and South America, Europe, not commonly collected ..... *L. tortilis* (Bolt.) Cooke (p. 129)
41. Pileus not striate, reddish brown; Kew Gardens ..... *L. nana* Massee (p. 111)

Type Studies

Although this study dealt primarily with North American taxa of *Laccaria,* it was necessary to try to examine the type collections of all names that have been treated in the genus. When no type existed, a lectotype or neotype was designated. A representative specimen was designated when no type material or material suitable for neotypification was available or when an illustration was lectotypified.

To clarify circumscriptions and stabilize application of names in *Laccaria,* Mueller and Vellinga (1986, 1990) and Mueller (1987) designated neotypes in cases where names lacked type specimens but were generally accepted and whose identity could be determined by common usage (Korf, 1982a,b). This was done even in cases where an illustration was included in the protologue. The International Code of Botanical Nomenclature (Greuter et al., 1988), however, now explicitly states that an illustration is part of the original material and must be chosen as a lectotype if no specimen suitable for lectotypification is available (Art. 7.5). This rule holds even though the circumscription of a fungus name often cannot be adequately defined without information on micromorphological characters. Those proposed neotypes (Mueller, 1987) that are now superfluous because the designated lectotype (illustration) takes precedence have been redesignated as "representative specimens." These specimens represent my interpretation of the name and are provided to fix the micromorphological characteristics of the epithet. Further clarification of the code regarding utilization of illustrations as lectotypes is needed because nomenclatural stability in the Agaricales, and other fungi, is often sacrificed by forcing workers to select illustrations as type specimens.

The importance of type studies was discussed by Ammirati and Ovrebo (1979). Some of the reasons given were ". . . to establish species concepts and relationships, to determine synonomy, and . . . for the development of a world-wide system of taxonomy for fleshy fungi" (Ammirati & Ovrebo, 1979). Additionally, they mentioned the importance of making detailed macro- and micromorphological information on each type collection available for workers involved in general studies.

The following type descriptions are arranged alphabetically by the final epithet, specific or infraspecific. Unless noted under Commentary, the type collection consists of more than one basidioma and is in an adequate state of preservation.

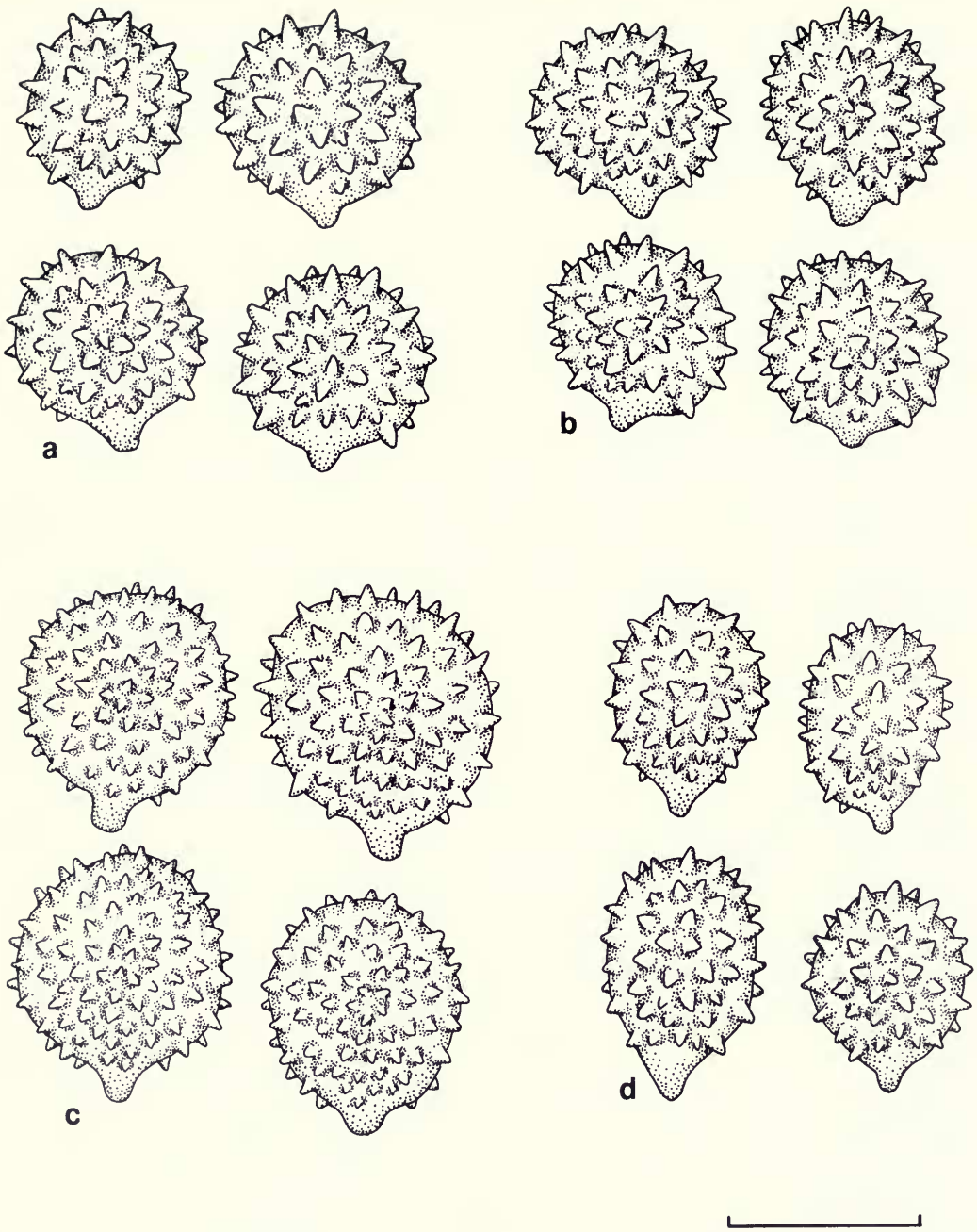


FIG. 59. Representative basidiospores from type specimens: **a,** *L. tetraspora* var. *aberrans* (holotype); **b,** *L. laccata* var. *affinis* (holotype); **c,** *L. altaica* (holotype); **d,** *L. amethysteo-occidentalis* (holotype). Scale line = 10 μm.

Laccaria tetraspora var. **aberrans** Singer, Bull. Soc. Mycol. France 83: 116. 1967. Figure 59a.

TYPE: Argentina, Neuquén, Parque Nacional de Nahuel Huapi, Camino a los Cántaros, 14 March 1959, *Singer M1774* (BAFC!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—As in *L. tetraspora* var. *scotica.*

MICROMORPHOLOGY (*Mihi*)—**Lamellar trama** parallel; hyphae mostly 3.5–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undif-

ferentiated. **Basidia** (N = 15) 33–44 × 10–13 μm, clavate, hyaline; sterigmata 4, up to 8.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7–8.7(–9) × 7–8.7(–9.2) μm ($\bar{x}$ = 7.9 ± 0.6 × 7.8 ± 0.6 μm), Q = 1–1.05(–1.12) ($\bar{Q}$ = 1.01 ± 0.03), globose, occasionally subglobose, hyaline, echinulate; echinulae (0.9–)1.4–1.8 μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3.5–8 μm diam., long-celled, morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—The type collection is infested with an "*Aspergillus*-like" fungus, with numerous conidia and conidiophores present. Because of this, no observations on the arrangement of the pileipellis hyphae or morphology of cheilocystidia could be made. Singer (1967) separated this variety from *L. tetraspora* var. *scotica* on the smaller basidiospores of *L. tetraspora* var. *aberrans,* shorter basidiospore ornamentation, and difference in habitat. *Laccaria tetraspora* var. *aberrans* was found on humus while *L. tetraspora* var. *scotica* fruited among *Sphagnum.*

This taxon is treated as a synonym of *L. ohiensis.*

Laccaria laccata var. **affinis** Singer, Bull. Soc. Mycol. France 83: 111–112. 1967. Figure 59b.

TYPE: England, Bedgebury, Kent, National Pine Arboretum, 30 October 1960, *Singer C 3118* (BAFC!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 30–48 mm broad, convex, centrally depressed, glabrous, distinctly fibrillose-asperulate under hand lens as in *Hygrocybe miniata,* slightly striate when moist, hygrophanous, uniform brownish rose color, fading to pale leather rose color when dehydrated; margin often crenulate-furrowed. **Lamellae** 5–6 mm broad, sinuate to decurrent, slightly serrate, often anastomosing and wrinkled, dull rose-colored, not as dull brownish color as in *L. laccata* var. *anglica*; lamellulae wrinkled. **Stipe** 80–110 × 5–6.5 mm, equal or nearly so, fibrillose, longitudinally striate, brownish rose-colored ("*brun fauve roussatre,*" Singer); striations very pale. **Basal mycelium** white. **Basidiospores** pure white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles usually composed of 5–15 hyphae; terminal cells of fascicular hyphae (N = 10) 37–55 × 6.5–13.5 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–8 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 29–47 × 9–12.5 μm, clavate, hyaline; sterigmata 4, up to 9.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 24.5–46 × (2–)3–5.5 μm, filamentous to subcapitate, occasionally strangulated, scattered, thin-walled, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) (7–)7.8–10 × (7–)7.8–10 μm ($\bar{x}$ = 8.6 ± 0.8 × 8.6 ± 0.8 μm), Q = 1–1.05 ($\bar{Q}$ = 1 ± 0.1), globose, rarely subglobose, hyaline, echinulate; echinulae 1–1.4 μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–7 μm diam., filamentous, tightly interwoven, hyaline.

COMMENTARY—The macro- and micromorphology of this collection fit within the circumscription of *L. laccata* var. *pallidifolia.* Bon (1983) proposed *L. affinis* (Singer) Bon based on this holotype, but data obtained to date do not support the recognition of it as a discrete variety or species. Although homokaryotic isolates of *Laccaria laccata* var. *pallidifolia* from North America and Sweden are intersterile (Mueller, 1991c), morphological differences have not been uncovered to recognize separate taxa for these intersterile populations. Until evidence of morphological or molecular divergence is obtained, this taxon is treated as a synonym of *L. laccata* var. *pallidifolia.*

Agaricus alpestris Britzelmayr, Hymenomyc. Südbayern VIII: 4, fig. 442. 1894.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Britzelmayr, *ibid.*)—**Pileus** fleshy; margin crenulate. **Lamellae** whitish or yellowish red-brown. **Stipe** bent.

MICROMORPHOLOGY (*Teste* Britzelmayr, *ibid.*)—**Basidiospores** 3–4 μm diam., rough, yellowish.

COMMENTARY—The protologue stated that this taxon was similar to *A. laccatus.* The basidiospore dimensions, however, fall well outside the range of basidiospore size for *Laccaria.*

Laccaria altaica Singer, Bull. Soc. Mycol. France 83: 122. 1967. Figure 59c.

TYPE: USSR, Kuraika, 31 July 1937, *Singer A439* (LE!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—Similar to *Laccaria echinospora* (Speg.) Singer.

MICROMORPHOLOGY (*Mihi*)—**Lamellar trama** parallel; hyphae thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 38–62 × 11.5–16 μm, clavate, hyaline; sterigmata 2(–4), up to 11.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (8.3–)11.5–14.5 (–15.6) × (8.3–)10–13.8 μm ($\bar{x}$ = 12.8 ± 1.5 × 11.5 ± 1 μm), Q = 1–1.2(–1.28) ($\bar{Q}$ = 1.12 ± 0.07), globose, subglobose, broadly ellipsoid or occasionally ellipsoid, hyaline, echinulate; echinulae 0.3–1 μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** not present.

COMMENTARY—The name, without a description, was originally published by Singer (1949). Owing to the extremely poor condition of the type collection, with only a few gill fragments extant, no comments can be made concerning macromorphological and many micromorphological characters.

Laccaria altaica is a later homonym of *L. pumila* (Mueller & Vellinga, 1986).

Laccaria amethysteo-occidentalis G. M. Mueller, Mycotaxon 20: 103. 1984. Figure 59d.

TYPE: Canada, British Columbia, near Squamish, Alice Lake Prov. Park campground, 3 October 1981, *G. M. Mueller 1256* (TENN 42526) (TENN!, holotype).

MACROMORPHOLOGY (*Mihi*)—**Pileus** 10–33 mm broad ($\bar{x}$ = 20 mm), convex becoming plane, occasionally depressed, not striate, finely fibrillose to fibrillose, deep purple ("Taupe Brown" to "Dull Indian Purple"); margin decurved, entire; context purple ("Dark Slate-Violet") with lighter gray-purple to white areas intermixed ("Pale Bluish Lavender"). **Lamellae** adnate to arcuate, distant, thick, < 5 mm broad, violaceous ("Deep Slate Violet" to "Slate-Violet"). **Stipe** 18–87 × 4–12 mm ($\bar{x}$ = 50 × 7.3 mm), equal or tapering toward apex, occasionally bulbose, dry, fibrillose, longitudinalstriate, purple ("Dark Slate-Purple," "Dark Vinaceous Brown," or "Hay's Brown"), often with lighter violet to white streaks ("Pale Bluish Lavender"); context solid, concolorous with pileus context. **Basal mycelium** violet ("Dark Slate-Purple" to "Deep Slate-Violet"). **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of tightly interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles usually composed of 15–30 hyphae; terminal cells of fascicular hyphae (N = 10) 30–73.5 × 8–15 μm, filamentous to clavate, occasionally broadly clavate; walls up to 0.5 μm thick, vinaceous brown; contents hyaline to light vinaceous brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light vinaceous brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–11.5 μm diam., thin-walled, hyaline to light vinaceous brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 36.5–50.5 × 9.5–15 μm, clavate, hyaline, vinaceous brown in mass; sterigmata 4, up to 8 μm long. **Pleurocystidia** lacking. **Cheilocystidia** lacking. **Basidiospores** (excluding ornamentation) (N = 30) 7.8–9.7 × 6–8.3 μm ($\bar{x}$ = 8.7 ± 0.6 × 7.3 ± 0.7 μm), Q = (1.05–)1.11–1.33(–1.36) ($\bar{Q}$ = 1.19 ± 0.08), subglobose to broadly ellipsoid, occasionally ellipsoid to amygdaliform, echinulate; echinulae 0.9–1.4 μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2.5–6.5 μm diam., hyaline, morphologically undifferentiated.

SOMATIC CULTURE MAT MORPHOLOGY—See the description presented in the treatment of *L. amethysteo-occidentalis* in the section on North American taxa.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

Laccaria amethystina Cooke, Grevillea 12: 69–70. 1884. Figure 60a.

TYPE: England, Devon, Dartmoor, Two Bridges, Whistmans Wood, 6 September 1971, *D. N. Pegler s.n.* (as *L. amethystea*) (K! neotype *fide* Mueller & Vellinga, 1990).

MACROMORPHOLOGY—Not provided.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered ± perpendicular individual hyphae or small fascicles of 2–3 ± perpendicular hyphae; terminal hyphae 43–60 × 9–

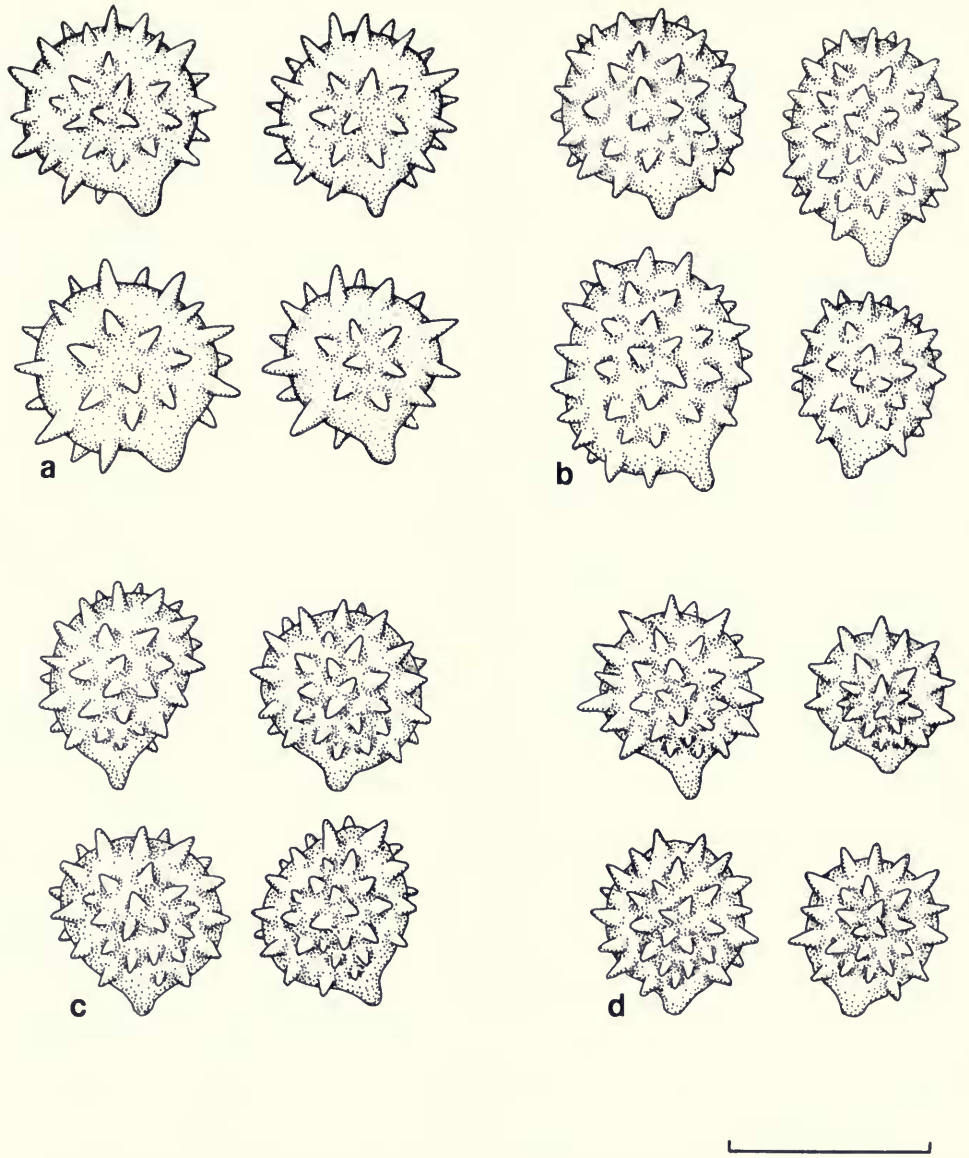


FIG. 60. Representative basidiospores from type or representative specimens: **a,** *L. amethystina* (neotype); **b,** *L. laccata* var. *anglica* (holotype); **c,** *L. laccata* var. *bicolor* (representative collection); **d,** *L. masonii* var. *brevispinosa* (holotype). Scale line = 10 μm.

16 μm, subclavate, clavate or strangulate, hyaline; walls up to 0.5 μm thick. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline. **Lamella trama** parallel; hyphae 3–8 μm diam., thin-walled, hyaline; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 37–55 × 11–16 μm, clavate, hyaline; sterigmata 4, up to 11 μm long. **Pleurocystidia** lacking. **Cheilocystidia** 40–70 × 6–12 μm, filamentous, strangulate or subclavate, thin-walled, numerous, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) (8.3–)8.7–9.7(–10) × 8.3–9.7(–10) μm ($\bar{x}$ = 9.2 ± 0.4 × 9.2 ± 0.4 μm), Q = 1–1.05 ($\bar{Q}$ = 1.01 ± 0.02), globose, echinulate; echinulae 1–1.8(–2.3) μm long, up to 1.2 μm wide at base; hilar appendix up to 1.4 μm long, prominent, truncate; plage present; contents occasionally uniguttulate.

COMMENTARY—The collection designated as neotype was selected from material requested from several herbaria. Original material or other col-

lections seen by Hudson were not located. As stated in Mueller and Vellinga (1990), the chosen collection fits Hudson's protologue and was collected in England.

This taxon is treated in detail in the section on North American taxa.

Laccaria laccata var. **anglica** Singer, Bull. Soc. Mycol. France 83: 110–111. 1967. Figure 60b.

TYPE: England, Kent, Bedgebury, National Pine Arboretum, 20 October 1960, *Singer C3119* (BAFC!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 25–37 mm, convex, plane or depressed at disc, often umbonate, pellucid-striate when fresh, occasionally radially sulcate at margin, finely tomentose to tomentose-fibrillose, strongly hygrophanous, reddish brown, fading to pale beige-red or pale dull rose, finally to pale mouse; disc rust-red. **Lamellae** sinuate to adnate, occasionally subventricose, subcrowded, moderately broad, rose to dull rose. **Stipe** 45–100 × 2.8 mm, equal or tapering toward apex, tomentose, especially apically, hollow, subhygrophanous, brown to reddish brown. **Basal mycelium** pure white. **Basidiospores** pure white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae (N = 10) 41.5–53 × 7.5–14 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel; hyphae mostly 3.5–9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 30–44 × 8–14 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7.4–)7.8–9.2(–9.7) × (7.4–)7.8–9.2(–9.7) μm ($\bar{x}$ = 8.4 ± 0.6 × 8.3 ± 0.6 μm), Q = 1–1.06 ($\bar{Q}$ = 1.01 ± 0.02), globose, occasionally subglobose, hyaline, echinulate; echinulae (1–)1.4–1.8 μm long, crowded; hilar appendix 1.2–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–10.5 μm diam., morphologically undifferentiated, tightly interwoven, hyaline; cells filamentous or barrel-shaped.

COMMENTARY—Although the basidiospore size and shape presented here fit the original circumscription, the length of basidiospore ornamentation observed in this study was larger than that reported by Singer (1967). Additionally, he reported numerous cheilocystidia ("cheilocystides et cystidioles nombreuses pres de l'arete, verforme, le plus souvent filamenteuses-subclaviculees, simple ou fourchues-ramifiees, 17–29 × 3–4, 7 μ") that I did not observe.

This taxon is treated as a synonym of *L. laccata* var. *pallidifolia*.

Agaricus bellus Persoon, Synopsis Methodica Fungorum. p. 452. 1801.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Persoon, *ibid.*)—**Pileus** fleshy, umbilicate, squamulose, yellow. **Lamellae** decurrent-toothed, distant. **Stipe** 25 mm long, thin, tough, lighter colored than pileus.

COMMENTARY—No authentic material of *A. bellus* could be found at L, LG, or GOET. Berkeley and Broome (1883) included this name in *Laccaria*, and other workers, including Rea (1922), concurred. Rea (1922) viewed this taxon as one with a dark yellow or golden pileus with darker squamules, a bright yellow stipe, and relatively small (7 × 5–7 μm), minutely warted basidiospores. Dennis et al. (1960) did not treat this taxon in their checklist. Based on the protologue, this taxon is not a *Laccaria*. Without micromorphological data, however, it is impossible to assign it to another genus.

Laccaria laccata var. **bicolor** Maire, Publ. Inst. Bot. Barcelona 3: 84. 1937. Figure 60c.

TYPE: Spain, Catalonia, Collado de Tosses, 7 October 1933, *Maire s.n.* (MPU!, holotype).

MACROMORPHOLOGY (*Teste* Maire, *ibid.*)—**Pileus** reddish, squamulose. **Lamellae** distant, lilac. **Stipe** reddish. **Basal mycelium** woolly, violet.

COMMENTARY—The single basidiocarp of the type collection is severely contaminated by an "*Aspergillus*-like" fungus. Because of distortion caused by the parasite, no micromorphological data could be obtained. My concept of the taxon is

based, therefore, on Maire's description and on the common usage of the name (Korf, 1982a,b). The following description is presented to illustrate my concept of the taxon.

REPRESENTATIVE SPECIMEN—USA, Washington, King Co., near Redmond, Watermain Woods, 24 October 1981, *G. M. Mueller 1352* (TENN 42529) (TENN).

MACROMORPHOLOGY (*Mihi*)—**Pileus** 12–43 mm broad, convex, often depressed, not striate, fibrillose-scaly, occasionally scaly, hygrophanous, pinkish flesh color ("Onion-skin Pink"), fading to ("Salmon-Buff"); margin decurved, entire to undulate, becoming eroded. **Lamellae** adnate-arcuate, moderately distant, thick, light vinaceous to light pinkish flesh color ("Pale Purplish Vinaceous," "Pale Congo Pink," or "Light Congo Pink"). **Stipe** 48–120 × 3–10 mm, equal with bulbous base, occasionally slightly clavate, dry, fibrillose, longitudinal-striate, light pinkish flesh color ("Flesh Pink"); striations darker ("Cacao Brown" to "Pecan Brown"). **Basal mycelium** copious, hygrophanous, when fresh violet ("Pale Vinaceous-Lilac"), becoming white.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae (N = 10) 37–76 × (6–)10–17.5 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3.7–6 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 33–43.5 × 9.7–12 μm, clavate, hyaline; sterigmata 4, up to 6.4 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 29–50 × 2.3–3.7 μm, filamentous to subclavate, abundant, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) 7–8.3 × (6–)6.4–7.8 μm ($\bar{x}$ = 7.6 ± 0.4 × 7.1 ± 0.5 μm), Q = 1–1.16 ($\bar{Q}$ = 1.07 ± 0.05), subglobose to broadly ellipsoid, rarely globose, hyaline, echinulate; echinulae 0.9–1.8 μm long, crowded; hilar appendix 1.3–1.9 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 5–9.8 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.

SOMATIC CULTURE MAT MORPHOLOGY (representative specimen)—**PDA: Radius** at week 3 = 14–19 mm, week 6 = 23–30 mm; **mat** felty, thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, becoming furrowed because of irregular infolding near plug, not translucent, dark, bright violet, fading to light orange-brown, by week 6 violet only in 3–4 mm band near margin, most of mat light orange-brown; aerial hyphae light grayish violet; **margin** 1–2 mm broad, subfelty, thin, light violet; **plug** violet, becoming light orange-brown; **hyphae** mostly morphologically undifferentiated, occasionally irregularly swollen, purplish brown in mass. **MMN: Radius** at week 3 = 37–45 mm, week 6 = 58–64 mm; **mat** subfelty to silky, thin, loosely interwoven, tightly appressed to agar surface, translucent light violet, becoming buff-colored; **margin** 1–2 mm broad, subfelty to silky, thin, even to serrate, light violet; **plug** concolorous; **hyphae** morphologically undifferentiated. **MEA: Radius** at week 3 = 32–43 mm, week 6 = 68–76 mm; **mat** subfelty to felty near plug, thick, tightly interwoven, tightly appressed to agar surface, subtranslucent, white; **margin** subfelty, thin, loosely interwoven, uneven, white; **plug** white; **hyphae** undifferentiated.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

Laccaria masonii var. **brevispinosa** McNabb, New Zealand J. Bot. 10: 466–467. 1972. Figure 60d.

TYPE: New Zealand, Nelson, Lake Daniels track, 16 May 1969, *McNabb PDD 29641* (PDD!, holotype).

MACROMORPHOLOGY (*Teste* McNabb, *ibid.*)—Pileus 5–35 mm broad, convex to plano-convex, occasionally plane at maturity, glabrous or minutely furfuraceous at disc, translucent striate at margin, hygrophanous, violaceous with buff tints when young, fading to buff at maturity. **Lamellae** adnexed to adnate, distant, thick, ≤ 4 mm broad, pallid violaceous when young, becoming pallid brownish pink, occasionally with faint violaceous tints, glaucous. **Stipe** up to 100 × 1–2.5 mm, 3–6 mm diam. at base, tough, dry, longitudinally fibrillose-sulcate, violaceous when young, becoming buff at base, finally buff except for violaceous tints at apex. **Basal mycelium** pallid violaceous. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered small fascicles of ± perpendicular hyphae; fascicles composed of 5–10(–15) hyphae; terminal cells of fascicular hyphae

(N = 10) 33–62 × 5.5–13 μm, filamentous, swollen, subclavate or clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to moderate yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 2.5–7 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 29–39 × 7.8–11.5 μm, clavate, hyaline; sterigmata 4, up to 6.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 6–8.3(–9.2) × 6–8.3(–8.7) μm ($\bar{x}$ = 7.5 ± 0.8 × 7.2 ± 0.7 μm), Q = 1.13(–1.16) ($\bar{Q}$ = 1.04 ± 0.05), globose to subglobose, occasionally broadly ellipsoid, hyaline, echinulate; echinulae 1.4–1.8(–2.3) μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2.5–7.5(–15) μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—Although the basidiospore shape and size fit the original circumscription, I measured the size of the ornamentation as slightly longer than McNabb ("spines 1.2–1.5 μm long"). Additionally, McNabb (1972) reported the presence of cystidia ("paraphyses numerous, simple or sparingly branched, filamentous, to 3 μm diam., projecting beyond basidia"). This discrepancy is probably due to the poor preservation of the collection. The specimens appear to have been overdried, and consequently the material did not rehydrate well. Because of PDD policy, only half of the type collection was sent on loan. Thus, the possibility exists that more variation is present in the complete type collection than is described above.

Laccaria bullulifera Singer *in* Singer and Moser, Mycopath. Mycol. Appl. 26: 149. 1965.

TYPE: Mexico, Popocatepetl, 21 August 1957, *Singer M1581* (MICH, holotype).

MICROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Lamellar trama** parallel. **Basidia** 30–31 × 8.5–10 μm, 4-sterigmate. **Cheilocystidia** 14 × 9.3 μm, balloon-shaped to subglobose, hyaline. **Basidiospores** 7–9 × 6.3–7.7 μm (including ornamentation), globose to broadly ellipsoid, hyaline, echinulate; echinulae 0.3–0.9 μm long.

COMMENTARY—No material of this taxon could be located at MICH. Although validly published by Singer and Moser (1965), the full description was published earlier (Singer, 1957). Aguirre-Acosta and Pérez-Silva (1978) and Montoya-Bello et al. (1987) have included this taxon in their treatments of Mexican fungi.

This taxon appears to be most similar to *L. trichodermophora*. The large cheilocystidia and somewhat smaller basidioma size reported from collections of *L. bullulifera* delimit the two taxa. *Laccaria trichodermophora* has been reported from Mexico as *L. farinacea sensu* Singer (Aguirre-Acosta and Pérez-Silva, 1978; Montoya-Bello et al., 1987).

Laccaria calospora Singer, Sydowia 7: 7–8. 1973. Figure 61a.

TYPE: USA, Massachusetts, Waban, 21 June 1945, *Southwick s.n.* (FH!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 15–26 mm broad, convex, becoming depressed or concave, finely fibrillose-asperate, hygrophanous, dingy purple-violet ("Vinaceous Purple") fading to dingy violaceous brown, then to buff color ("Fawn Color" to "Army Brown"); margin frequently sulcate. **Lamellae** sinuate to arcuate, many-ranked, distant, 2–3 mm broad, purplish ("Amaranth" or "Wild Aster"). **Stipe** 38–50 × 3–9 mm, tapering toward apex, fibrillose, striate above, concolorous with pileus. **Basal mycelium** tomentose, ± concolorous with pileus. **Basidiospores** violaceous ("Pale Verbena Violet") in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with numerous fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae (N = 10) 32–69 × 8–11 μm, filamentous, clavate or capitate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 4–11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 32–46 × 8.5–13.5 μm, clavate, hyaline; sterigmata 4, up to 8.3 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 36.5–64.5 × 5.5–8 μm, filamentous to subclavate, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) 7.4–8.7 × 7–8.3

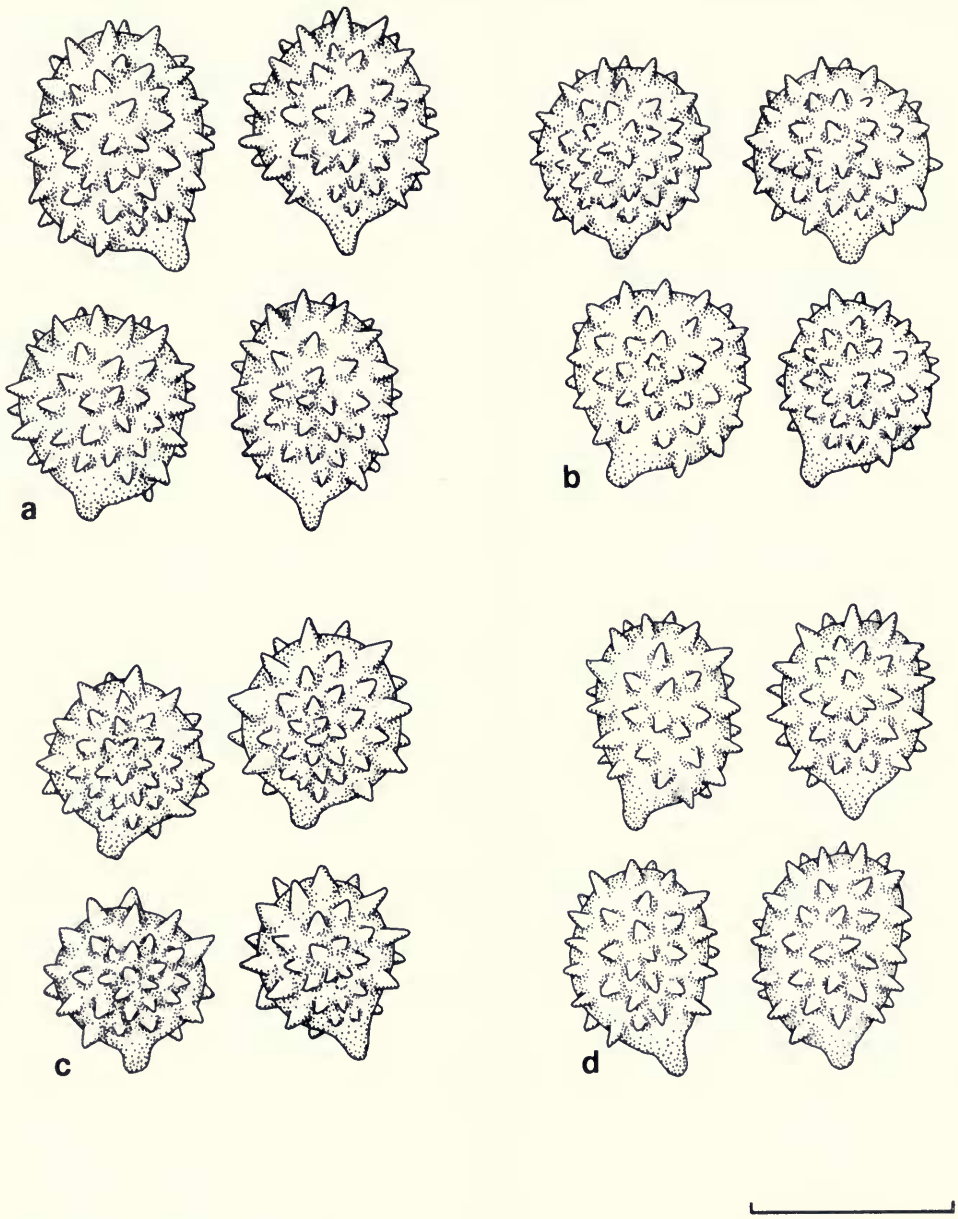


FIG. 61. Representative basidiospores from type specimens: **a,** *L. calospora* (holotype); **b,** *A. canaliculata* (holotype); **c,** *L. chibinensis* (holotype); **d,** *L. laccata* var. *chilensis* (holotype). Scale line = 10 μm.

μm ($\bar{x}$ = 8 ± 0.4 × 7.7 ± 0.5 μm), Q = 1–1.12 ($\bar{Q}$ = 1.03 ± 0.04), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae 1.4–2.3 μm long, crowded; hilar appendix 1.2–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–12 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

COMMENTARY—Mueller and Vellinga (1986, 1990) have treated this taxon as a synonym of *L. amethystina*. Although the type collection of *L. calospora* was collected in Massachusetts, Singer (1973) also listed a collection from Colombia. There is considerable variability in size and color among the violet specimens of *Laccaria* that I have collected in Costa Rica and Colombia. Mueller

and Singer (1988) recently recognized one of these as a segregate species, *L. gomezii*. It is possible that additional taxa will be proposed when the Neotropical species of *Laccaria* are revised. Thus, although *L. calospora* is currently treated as a synonym, its status may change with the accumulation of additional data.

Agaricus (Laccaria) canaliculata Cooke & Massee, Grevillea 18: 2. 1889. Figure 61b.

TYPE: Australia, Brisbane, no date, *Baily 710* (K!, holotype).

MACROMORPHOLOGY (*Teste* Cooke & Massee, *ibid.*)—**Pileus** submembranous, small, becoming umbilicate, velvety, radially sulcate, light brown; margin slightly crenulate. **Lamellae** adnate, subdistant, broad, flesh-colored, with a white dust. **Stipe** thin, equal, longitudinally fibrillose, becoming hollow, pallid.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae; hyphae up to 10.5 μm diam.; cells undifferentiated to barrel-shaped; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 3.5–9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 30.5–50.5 × 8–12.5 μm, clavate, hyaline; sterigmata 2(–4), up to 8 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7.4–9.7 × (7–)7.4–9.2(–9.7) μm ($\bar{x}$ = 8.6 ± 0.7 × 8.3 ± 0.7 μm), Q = 1–1.05(–1.17) ($\bar{Q}$ = 1.03 ± 0.05), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae 0.5–1.4 (–1.8) μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 8–20 μm diam., tightly interwoven, hyaline; cells barrel-shaped.

COMMENTARY—The type collection consists of a fragment from a single basidioma. Although Stevenson (1964) reported this taxon from New Zealand, McNabb (1972) stated that the material cited by Stevenson from New Zealand was referable to *L. glabripes*. McNabb's description of the holotype states that the basidia were 4-sterigmate. Likewise, May (1990) stated that he found the basisdia in the type specimen to be 4-sterigmate. Although I encountered a few 3- or 4-sterigmate basidia, the majority of basidia bore two basidiospores. I agree with Pegler's (1965) findings, therefore, and treat *L. canaliculata* as a bisterigmate taxon.

Laccaria laccata var. **carbonicola** Singer, Bull. Soc. Mycol. France 83: 110. 1967.

TYPE: USA, Massachusetts, Blue Hills, 11 November 1943, *Singer s.n.* (FH, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 10–30 mm broad, convex, becoming depressed, glabrous, translucent-striate when fresh, strongly hygrophanous, reddish fawn color when fresh. **Lamellae** adnexed or adnate, subdistant, broad, dull rose color. **Stipe** 40–60 × 3–7 mm, equal or tapering toward the apex, finely fibrillose, farinaceous at apex, concolorous with pileus, apex often paler. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Basidia** 40–47 × 9 μm, 4-sterigmate. **Cheilocystidia** not observed. **Basidiospores** 7.7–8.2 × 6.5–7.2 μm (including ornamentation); echinulae mostly 0.7 μm long.

COMMENTARY—The type collection could not be found at FH. The taxon is treated as a synonym of *L. laccata* var. *laccata*.

Laccaria chibinensis Michailovski, Mikologia Fitopatologia 8: 523. 1974. Figure 61c.

TYPE: USSR, Murmansk, 5 July 1973, *Michailovski s.n.* (LE!, holotype).

MACROMORPHOLOGY (*Teste* Mikhailovski, *ibid.*)—**Pileus** 20–40 mm broad, convex, then cushion-shaped, glabrous, not hygrophanous, dark ochraceous brown ("ochraceo-fuscidulus," Michail.), tinted with a light blue pruina ("vix coerulescenti-pruinosus," Michail.); margin entire. **Lamellae** decurrent, distant, thick, sublilac-ochraceous ("sublilacino-ochraceae," Michail.). **Stipe** 30–45 × 8–15 mm, subclavate, rarely entire, fleshy, subfibrose, hollow, concolorous with pileus, lacking pruina.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with numerous scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–30 hyphae; terminal cells of fascicular hyphae (N = 10) 23–53 × 5.5–10.5 μm, filamen-

tous, swollen, subclavate, clavate or capitate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 3–7 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 10) 33–46 × 9–11 μm, clavate, hyaline; sterigmata (2–)4, up to 6 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 27–50.5 × 2.3–4 μm, filamentous to subcapitate, abundant, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) 7–9.2 × 6.4–8.3 μm ($\bar{x}$ =8.1 ± 0.6 × 7.4 ± 0.5 μm), Q = 1–1.2 ($\bar{Q}$ = 1.09 ± 0.06), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae (0.8–)1.4–1.8 μm long, > 1.2 μm wide at base; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–12 μm diam., tightly interwoven, hyaline; cells filamentous or barrel-shaped.

COMMENTARY—Based on the original description, this taxon appears to be closest phenetically to the *L. amethystina* group.

Laccaria laccata var. **chilensis** Singer, Bull. Soc. Mycol. France 83: 109. 1967. Figure 61d.

TYPE: Chile, Valdivia, Cordillera Pelada, El Mirador, 5 May 1965, *Singer M5514* (BAFC!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 12–24 mm broad, convex, slightly applanate to depressed at center, glabrous, innately fibrillose under hand lens, occasionally rivulose in age, hygrophanous, rose brown, fading to ocher when dehydrated. **Lamellae** adnate, subdistant, broad, dull rose-colored. **Stipe** at least 2.5–3 times longer than diam. of pileus, tapering slightly toward apex, slightly fibrillose with longitudinal innate fibrils, stuffed, concolorous with pileus or browner. **Basal mycelium** pure white.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–15 hyphae; terminal cells of fascicular hyphae (N = 10) 33–60 × 4.5–10 μm, filamentous to subclavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 5–14 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. Basidia (N = 15) 31–42 × 7.5–11 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 6.4–7.8 × 6–7.4(–7.8) μm ($\bar{x}$ = 7.3 ± 0.4 × 6.7 ± 0.5 μm), Q = 1–1.16 ($\bar{Q}$ = 1.08 ± 0.06), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae (< 0.5–)1.4–1.8 μm long, crowded; hilar appendix 1.5–2.2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–14 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

COMMENTARY—The type collection consists of a single basidioma. Singer (1967) reported infrequent cheilocystidia ("Cheilocystides et cystidioles tres esparsed, filamenteuses ou versiformes").

This taxon is treated as a synonym of *L. laccata* var. *pallidifolia*.

Clitocybe laccata var. **decurrens** Peck, Annual Rep. New York State Bot. 157: 92. 1912. Figure 62a.

TYPE: USA, New York, Warren Co., Boltom Landing, August, *Peck s.n.* (NYS!, holotype).

MACROMORPHOLOGY (*Teste* Peck, *ibid*)—Differing from the type by its distinctly decurrent to arcuate-decurrent lamellae.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with numerous fascicles of ± perpendicular loosely interwoven hyphae; fascicles composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 30–55 × 4.5–9 μm, filamentous, subclavate, or rarely clavate; walls up to 0.5 μm thick, light yellowish brown; contents light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae usually 3.5–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 30–46 × 11–14.5 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 24–41 × 3–4.5 μm, filamentous to subcapitate, rarely branched, abundant, thin-walled, hy-

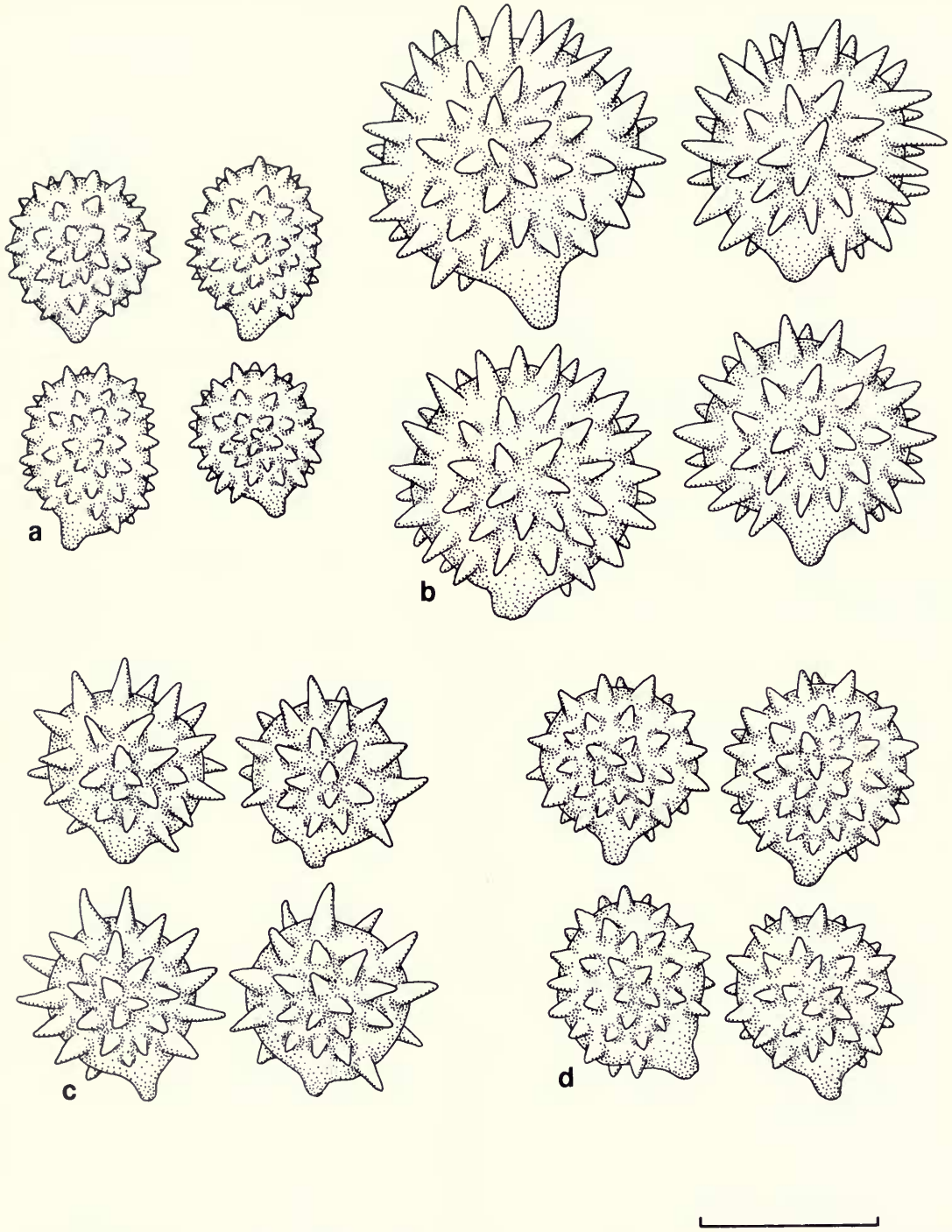


FIG. 62. Representative basidiospores from type specimens: **a,** *C. laccata* var. *decurrens* (holotype); **b,** *A.* (*Clitocybe*) *echinosporus* (holotype); **c,** *L. fibrillosa* (holotype); **d,** *A. fraternus* (holotype). Scale line = 10 μm.

aline. **Basidiospores** (excluding ornamentation) (N = 30) 7.4–9.2(–11.5) × 7–9.2(–10) μm ($\bar{x}$ = 8.6 ± 0.9 × 8 ± 0.8 μm), Q = 1–1.14(–1.24) ($\bar{Q}$ = 1.08 ± 0.07), globose to subglobose, occasionally broadly ellipsoid, hyaline, echinulate; echinulae (0.5–)1.0(–1.4) μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–8 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—This taxon is treated as a synonym of *L. laccata* var. *pallidifolia*.

Agaricus echinospermus Britzelmayr, Hymenomyc. Südbayern, Bot. Centralbl. 54: 5–6, figs. 512, 518. 1893.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Britzelmayr, *ibid.*)—**Pileus** glabrous to slightly fibrillose, somewhat translucent, yellowish brown to brown. **Lamellae** adnate, crenate, whitish to brownish. **Stipe** solid, yellowish brown to brown, lighter underneath.

MICROMORPHOLOGY (*Teste* Britzelmayr, *ibid.*)—**Basidiospores** 6–8 μm diam., angular spined.

COMMENTARY—The protologue stated that this taxon was similar to *A. echinosporous*. The basidiospore dimensions provided are much smaller than those of *A. echinosporous*, but without additional micromorphological data, it is impossible to tell if the dimensions provided are correct.

This taxon is treated as a synonym of *L. tortilis*.

Agaricus (Clitocybe) echinosporus Spegazzini, Anales Soc. Ci. Argentina 10: 123. 1880. Figure 62b.

TYPE: Argentina, La Baea, May 1880, *Spegazzini 2891* (LPS!, holotype).

MACROMORPHOLOGY (*Teste* Spegazzini, *ibid.*)—**Pileus** 5–10 mm broad, hemispheric, becoming plano-convex, centrally depressed, radially sulcate, pellucid, subhygrophanous, rose-colored; disc darker; margin straight, undulate to subcrenulate. **Lamellae** acute at apex, long decurrent, distant, thick, fleshy, up to 2.5 mm broad, entire, paler than pileus. **Stipe** 10–15 × 1.5–3.5 mm, subclavate, terete, fragile, fibrous-fleshy, rose-colored.

MICROMORPHOLOGY (*Mihi*)—**Lamellar trama** parallel; hyphae mostly 3–12 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 9) 39–64 × 10–14 μm, clavate, hyaline, not rehydrating well; sterigmata 2, up to 11 μm long, stout. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 11–13.8(–15.6) × 11–14.7 μm ($\bar{x}$ = 12.5 ± 1.1 × 12.4 ± 1.0 μm), Q= 1–1.06 ($\bar{Q}$ = 1.01 ± 0.02), globose, occasionally subglobose, hyaline, echinulate; echinulae 2.3–3.2(–3.7) μm long, 1.3–1.8 μm wide at base, very crowded; hilar appendix 1.5–2.3 μm long, prominent, truncate; plage present; contents often uniguttulate.

COMMENTARY—The type collection consists of a fragment from a single, small pileus. Observations could not be made on arrangement of pileipellis hyphae or on stipe characteristics. No cystidia were observed although the original description reported them ("basidia . . . 55–60 × 10, cystidiis major . . ."). The discrepancy between Spegazzini's and my description may be due to poor rehydration or to the absence of cystidia in the micromorphological preparations examined.

This taxon is treated as a synonym of *L. tortilis*. Refer to the Observations under *L. tortilis* in the section on North American taxa for a discussion of conflicting interpretations of these two taxa.

Laccaria fibrillosa McNabb, New Zealand J. Bot. 10: 468–469. 1972. Figure 62c.

TYPE: New Zealand, Nelson, Lake Daniels track, 15 May 1969, *McNabb PDD 29639* (PDD!, holotype).

MACROMORPHOLOGY (*Teste* McNabb, *ibid*)—**Pileus** 5–35 mm broad, strongly convex, becoming convex to plano-convex, umbonate, radially fibrillose, disc scurfy, fibers aggregated toward margin, hygrophanous, buff with faint violaceous tints, fibrils dark brown to brownish black at disc, paler toward margin; margin dentate to lacerate with age. **Lamellae** adnexed to adnate, distant, > 5 mm broad, pallid violaceous, becoming buff with age, glaucous. **Stipe** 20–70 × 1.5–3 mm, equal or slightly expanded at base, tough, dry, hollow, longitudinally fibrillose-striate, pallid, violaceous when young, fading to buff from base upward, at maturity buff with violaceous tints at extreme apex. **Basal mycelium** pallid violaceous. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** composed of ± parallel, radially arranged hyphae cov-

ering disc, separating toward margin, yielding an appearance similar to spokes of a wheel; hyphal elements (N = 10) 33–60 × 6–10 μm; cells barrel-shaped; walls up to 0.5 μm thick, light yellowish brown; contents dark brown in mass. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline to light yellowish brown. **Lamellar trama** parallel to subparallel; hyphae 2.5–9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 38.5–60 × 9–14 μm, clavate, hyaline; sterigmata 4, up to 7.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7–8.7 × 7–8.7 μm ($\bar{x}$ = 8.9 ± 0.6 × 8.8 ± 0.6 μm), Q = 1–1.12 ($\bar{Q}$ = 1.02 ± 0.04), globose to subglobose, hyaline, strongly echinulate; echinulae (1.4–)1.8–2.3(–2.8) μm long, not crowded; hilar appendix 1.4–2 μm long, prominent, truncate; plage present; contents usually uniguttulate. **Basal mycelium hyphae** mostly 2.5–9 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—McNabb (1972) reported that the pileipellis was "composed of unspecialized, repent, interwoven, thin-walled, clamped hyphae. . . ." This discrepancy may be due to poor rehydration in the material I examined. In longitudinal section, the arrangement of pileipellis hyphae was not discernible, so the data presented here were based on a whole mount of a scalp section. Owing to PDD policy, only half of the type collection was sent on loan. The possibility exists that more variation is present in the entire type collection than is described above.

Two taxa were included in Stevenson's (1964) original description and illustration of *L. masonii*. The type collection consists entirely of basidiomata with glabrous pilei and the epithet *L. masonii* is restricted to that circumscription. McNabb (1972) proposed *L. fibrillosa* to represent the other taxon included in the protologue.

Laccaria flavobrunnea Lebedeva, Opredelitel' Shlyapochykh Gribov. p. 350. 1949.

TYPE: lacking.

COMMENTARY—No authentic material of this taxon was included with the material loaned from LE. In addition, I have not located a copy of the original description. At this time, therefore, I cannot make any comments regarding its affinities to other *Laccaria*.

Agaricus flavofuscus Britzelmayr, Hymenomyc. Südbayern VIII: 4, fig. 441. 1894.

MACROMORPHOLOGY (*Teste* Britzelmayr, *ibid.*)—**Lamellae** white or brownish.

MICROMORPHOLOGY (*Teste* Britzelmayr, *ibid.*)—**Basidiospores** smooth.

COMMENTARY—The protologue stated that this taxon was very similar to *A. alpestris* and that it was difficult to tell the two apart. Based on the report that the basidiospores are smooth, *A. flavofuscus* cannot be a *Laccaria*. As stated in the Commentary under *A. alpestris*, I also do not treat that taxon as a *Laccaria*.

Agaricus fraternus Cooke & Massee, Grevillea 16: 31. 1887. Figure 62d.

TYPE: Australia, vic. Port Phillip, *French No. 1* (K!, holotype).

MACROMORPHOLOGY (*Teste* Cooke & Massee, *ibid.*)—**Pileus** convex, depressed, umbilicate, smooth, glabrous, dark rusty-red. **Lamellae** broad, subdistant, adnate, rusty-red color. **Stipe** elongate, thin, tapering toward apex, glabrous, hollow, concolorous with pileus.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; individual hyphae not discernible, dark yellowish brown in mass. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 3–10 μm diam., thin-walled, hyaline to light yellowish brown. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 29–44 × 8–12 μm, clavate, hyaline; sterigmata 2, up to 11 μm long, stout. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (8.3–)9.2–11(–11.5) × 8.7–10.6(–11.5) μm ($\bar{x}$ = 9.9 ± 0.7 × 9.9 ± 0.7 μm), Q = (0.95–)1–1.06(–1.09) ($\bar{Q}$ = 1.01 ± 0.03), globose to subglobose, hyaline, echinulate; echinulae (0.9–)1.4–1.8 μm long, crowded; hilar appendix 1.3–2.8 μm long, prominent, truncate; plage present; contents often uniguttulate.

COMMENTARY—The type collection consists of a fragment from one pileus and a short segment of a stipe. Individual hyphae of the pileipellis were not discernible because of poor rehydration.

Tom W. May (University of Melbourne, pers. comm.) reports the finding of a potentially paratypic collection at MEL that better fits the protologue but that is not contaxic with the type specimen housed at K. It has been assumed that the report of ellipsoid basidiospores in the original diagnosis of *A. fraternus* probably referred to another collection on the type sheet at K that was collected in New Zealand (Pegler, 1965; Mueller & Vellinga, 1986). If the collection housed at MEL is lectotypified, *A. fraternus* would not fit into the generic circumscription of *Laccaria* and the correct basionym for the taxon treated here would be *N. goossensiae.*

This taxon is treated in detail in the section on North American taxa.

Laccaria galerinoides Singer *in* Singer and Moser, Mycopath. Mycol. Appl. 26: 147–148. 1965. Figure 63a.

TYPE: Chile, Valdivia, Cordillera Pelada, 930–1000 m alt., 28 March 1963, *Singer M3212* (BAFC!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 16–17 mm broad, convex, centrally depressed, glabrous, translucent striate, occasionally sulcate, light ochraceous-brown ("Peruvian Br." M&P) to golden-ochraceous ("Inca Gold" M&P) at margin, becoming sordid ("Leather Br." M&P). **Lamellae** adnate, crowded to subdistant, moderately thick, entire, pallid ochraceous-isabelline ("Grain" M&P), becoming pallid ("Avellaneous-Argillaceous" M&P), 2-ranked; lamellulae narrow. **Stipe** 95–115 × 2–5 mm, glabrous, tubular, with distinct superficial innate striations, radicating, ochraceous-brown ("Titan" M&P), red-brown ("Chutney" M&P) or almost black, much lighter toward apex. **Basal mycelium** pallid.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae (N = 10) 37–57.5 × 6.5–12 μm, filamentous, subclavate or rarely clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel; hyphae mostly 4–19 μm diam., thin-walled, hyaline to light yellowish brown. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 29–40 × 9–11 μm, clavate, hyaline; sterigmata 4, up to 6.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7.4–9.7(–10) × 5.5–7.8 μm ($\bar{x}$ = 8.5 ± 0.7 × 6.3 ± 0.6 μm), Q = 1.16–1.52 ($\bar{Q}$ = 1.34 ± 0.08), ellipsoid to amygdaliform, rarely subglobose, hyaline, echinulate; echinulae 0.9–1.4(–1.8) μm long, not crowded; hilar appendix 1.5–2.3 μm long, very prominent, truncate; plage present; contents occasionally uniguttulate.

COMMENTARY—The type collection consists of a single basidioma lacking the stipe base. The basidiospores observed were larger than those reported by Singer (Singer & Moser, 1965) ("sporis 7–8 × 5,7–6,8 μ"). In his unpublished notes on this specimen, however, Singer gives the basidiospore size as 6.8–10 × 5–7.5 μm including echinulae. Additionally, Singer (Singer & Moser, 1965) reported sparse cheilocystidia ("cheilocystiis sparsis, ad nec non prope aciem visis, hyalinis, ± 2,5 μ latis").

I have collected this taxon from the type locality as well as additional locations in southern Chile and Tierra del Fuego. My findings fit those given for the taxon by Horak (1979). Although Singer (1986) placed *L. galerinoides* in its own stirps, this does not appear justified, based on my study of the type and the subsequent material examined. See observations under *L. longipes* in the section on North American taxa for additional data.

Laccaria laccata var. **gibba** Singer, Beih. Nova Hedwigia 29: 27. 1969. Figure 63b.

TYPE: Chile, Valdivia, Cordillera Pelada, 6 May 1967, *Singer M6738* (SGO!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 10–16 mm broad, convex, becoming plane, umbonate, glabrous, when dry with innately appressed fibers, radially pellucid-striate, sulcate, hygrophanous, reddish brown (between 14 A 11 and 5 C 11 M&P); margin light flesh color (11 C 7 and 12 E 8 M&P). **Lamellae** adnate, adnate-decurrent, or decurrent, distant, broad, rose-colored (between 3 A 10 and 9 A 6 M&P). **Stipe** 45–50 × 2–2.5 mm, equal or narrowed at apex, glabrous when moist, hygrophanous, dark red (6 J 12 M&P); apex lighter in color. **Basal mycelium** white.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae, no fascicles of hyphae observed; terminal hyphal cells (N = 10) 38–67 × 7–18 μm, subclavate to clavate, light yellowish brown in

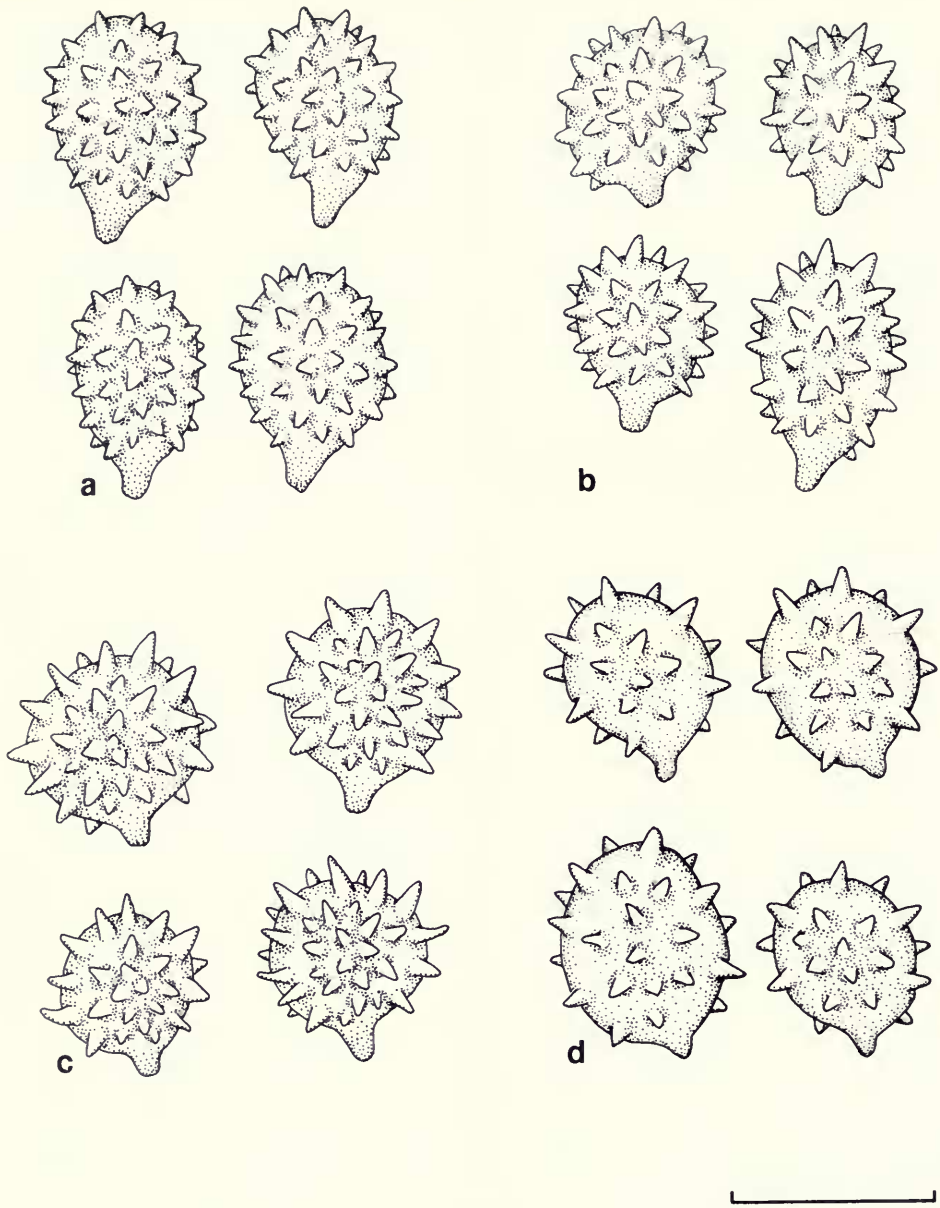


FIG. 63. Representative basidiospores from type specimens: **a,** *L. galerinoides* (holotype); **b,** *L. laccata* var. *gibba* (holotype); **c,** *L. glabripes* (holotype); **d,** *L. gomezii* (holotype). Scale line = 10 μm.

mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae thin-walled, hyaline to light yellowish brown. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 29–48 × 7.5–11 μm, clavate, hyaline; sterigmata (2–)4, up to 7 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7–8.7 × (5–)6–7.4 μm ($\bar{x}$ = 7.8 ± 0.5 × 6.3 ± 0.5 μm), Q = 1.08–1.35 (–1.38) ($\bar{Q}$ = 1.25 ± 0.07), occasionally subglobose, usually broadly ellipsoid to ellipsoid, hyaline, echinulate; echinulae 0.9–1.8(–2.3) μm long, not crowded; hilar appendix 1.3–1.8 μm long,

prominent, truncate; plage present; contents occasionally uniguttulate.

COMMENTARY—The type collection consists of a single pileus and a segment of the stipe without the base. Singer (1969) reported shorter basidiospore ornamentation ("spinulis 0,3–0,9 μ proji-cientibus") than presented here. As the specimen lacked lamellar margins, no observation of cheilocystidia was possible. Singer (1969) reported the cystidia as "inconspicuis subfilamentosis consistente."

This taxon is treated as a synonym of *L. laccata* var. *laccata.*

Laccaria glabripes McNabb, New Zealand J. Bot. 10: 477–478. 1972. Figure 63c.

TYPE: New Zealand, Nelson, Lake Daniels track, 25 April 1969, *McNabb PDD 29640* (PDD!, holotype).

MACROMORPHOLOGY (*Teste* McNabb, *ibid.*)—**Pileus** 5–25(–35) mm broad, convex, becoming plano-convex, applanate, occasionally depressed, conspicuously pellucid-striate when wet, slightly sulcate, almost glabrous when wet, minutely furfuraceous when dry, hygrophanous, flesh pink to reddish brown, drying buff, disc darker; margin reflexed in age. **Lamellae** adnate to subdecurrent, distant, thick, up to 6 mm broad, intermixed, flesh pink, glaucous. **Stipe** 25–60 × 1.5–3.5 mm, equal, dry, glabrous, appearing cartillaginous when wet, not longitudinally fibrillose, reddish brown, concolorous with disc. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered small fascicles of ± perpendicular hyphae; fascicles composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 33–60 × 6–10 μm, filamentous, subclavate, subcapitate, or occasionally strangulate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 2.5–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 38.5–60 × 9–14.5 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7–8.7 × 7–8.7 μm ($\bar{x}$ = 7.9 ± 0.5 × 7.8 ± 0.5 μm), Q = 1–1.12 ($\bar{Q}$ = 1.02 ± 0.04), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae (1.4–)1.8–2.3(–2.8) μm long, > 1.2 μm wide at base, relatively crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–12 μm diam., tightly interwoven, hyaline; cells barrel-shaped.

COMMENTARY—Owing to PDD policy, only half of the type collection was sent on loan. The possibility exists that more variation is present in the complete type collection than is described above.

Collections referable to *L. striatula* were treated as *L. glabripes* in my dissertation (Mueller, 1982). Aguirre-Acosta and Pérez-Silva (1978) reported *L. glabripes* from Mexico, but I believe that their material is referable to *L. striatula.* As mentioned in the Commentary under *A. canaliculata,* T. W. May (1990, pers. comm.) treats *L. glabripes* as a synonym of *L. canaliculata.* As Pegler (1965) and I found the type of *L. canaliculata* to have 2-sterigmate basidia, I treat the two taxa as separate species, *L. glabripes* and *L. canaliculata.*

Agaricus (Clitocybe) glaucipes Berkeley & Curtis, Ann. Mag. Nat. Hist., III. 4: 284. 1859.

TYPE: USA, Connecticut, no date, *Curtis 5546* (collected by C. Wright) (K!, holotype).

MACROMORPHOLOGY (*Teste* Berkeley & Curtis, *ibid.*)—**Pileus** 25 mm broad, convex, thin, pubescent, pale rufous; margin incurved. **Lamellae** adnate, subdistant, white. **Stipe** 50 × 6 mm, solid, concolorous with pileus.

COMMENTARY—The type collection consists of one very moldy basidiocarp. No micromorphological observations could be obtained, and the original description does not include micromorphological data. The protologue stated that *A. glaucipes* was allied to *A. laccata,* and the epithet is treated as a synonym of *L. laccata* var. *laccata.*

Laccaria gomezii Singer & G. M. Mueller *in* Mueller and Singer, Mycotaxon 33: 224–225. 1988. Figure 63d.

TYPE: Costa Rica, Cartago Prov., along Panamerican Highway, km 55, La Chonta, 2800 m, under *Quercus* and *Magnolia,* September 1982, *Gómez 18443* (F!, holotype).

MACROMORPHOLOGY (*Teste* R. Singer, unpubl. notes)—**Pileus** 30 mm broad (when dried), convex with a deep umbilicus, squarrose in depression,

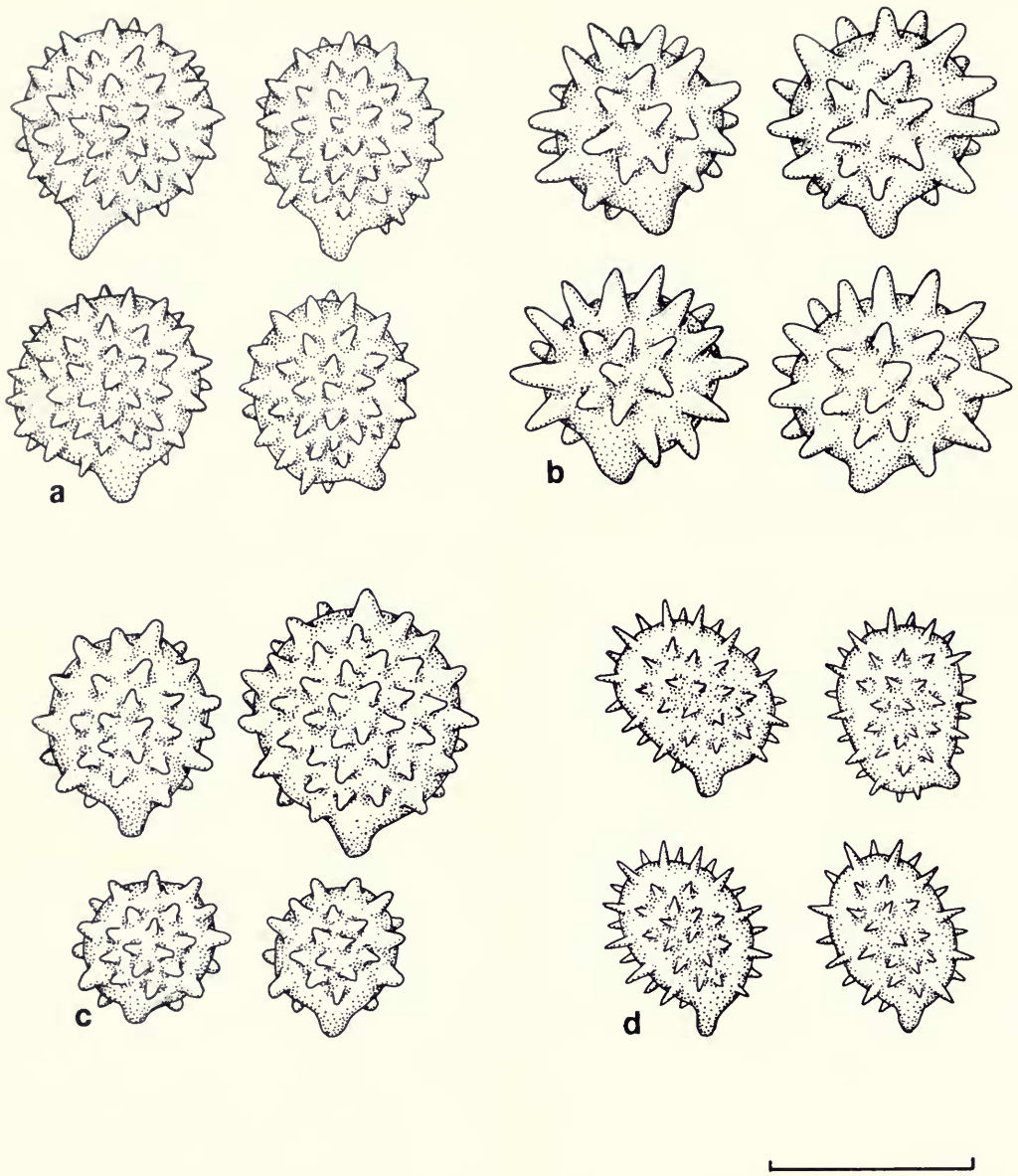


FIG. 64. Representative basidiospores from type specimens: **a,** *Naucoria goossensiae* (holotype); **b,** *C. tortilis* var. *gracilis* (holotype); **c,** *L. laccata* var. *intermedia* (holotype); **d,** *A. laccatus* (neotype). Scale line = 10 μm.

finely fibrillose-squamulose or squarrulose on the margin, not rimose or strongly radially fibrillose, light violet suffused with chocolate brown, dried uniformly "blondine" to "canbaak" (M&P). **Lamellae** adnate-subdecurrent, close, moderately broad, violet, somewhat whitish pulverulent under a lens when dry. **Stipe** 80 × 3–4 mm, pubescent to occasionally squamulose at apex, longitudinally sulcate when dry, coarsely woolly-strigose by the dried basal mycelium, appearing hispid in part and less distinctly violet than pileus. **Context** dirty white; odor and taste not annotated.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of tightly interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–30 hyphae; terminal cells of fasicular hyphae 12–15 μm diam., filamentous to subclavate, hyaline; walls up to 0.5 μm thick. **Pileus trama** tightly

interwoven, morphologically undifferentiated, hyaline. **Lamellar trama** parallel to subparallel; hyphae mostly 4–8 μm diam., thin-walled, hyaline. **Subhymenium** morphologically undifferentiated. **Basidia** 35–43 × 9–12 μm, clavate, hyaline; sterigmata 4, up to 10 μm long. **Pleurocystidia** lacking. **Cheilocystidia** 45–80 × 6–9 μm, subclavate, abundant, forming an early sterile layer, thin-walled, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) 7.8–9.3 × 7–7.8 μm ($\bar{x}$ = 8.7 ± 0.5 × 7.6 ± 0.4 μm), Q = 1.06–1.29 ($\bar{Q}$ = 1.14 ± 0.06), subglobose to broadly ellipsoid, rarely ellipsoid, hyaline, echinulate; echinulae 1–2.5 μm, ≤ 1 μm wide at base, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; contents occasionally uniguttulate. **Caulocystidia** 34–65 × 7–14 μm, subclavate, clavate or strangulate, thin-walled, hyaline to light vinaceous brown, formed from recurved surface hyphae, scattered or clustered in small groups at apex of stipe, absent or very infrequent below.

COMMENTARY—Specimens of this taxon have been collected in Costa Rica and Colombia. *Laccaria gomezii* occurs sympatrically with *L. amethystina,* with which it is morphologically similar. The two taxa are distinguished by basidioma color, lamellar thickness and attachment, and basidiospore shape. See Observations under *L. amethystina* in the section under North American taxa and Mueller and Singer (1988) for additional information.

Naucoria goossensiae Beeli, Bull. Soc. Roy. Bot. Belgique 61: 88. 1928. Figure 64a.

TYPE: Zaire, Ori, Noika, May 1926, *Goossens 558* (BR!, holotype).

MACROMORPHOLOGY (*Teste* Beeli, *ibid.*)—**Pileus** 25–35 mm broad, convex to umbilicate, glabrous, brownish rust color; margin incurved. **Lamellae** adnate or free, up to 7 mm broad, brownish red color. **Stipe** 45 × 4–5 mm, cylindrical, thickened at base, glabrous, hollow, concolorous with pileus.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–15 hyphae; terminal cells of fascicular hyphae (N = 5) 37–57.5 × 5–10.5 μm, filamentous, subclavate or clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 2.5–10 (–16) μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 28–44 × 9–12.5 μm, clavate, hyaline; sterigmata 2(–4), up to 14 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7.8–)8.7–11 (–11.5) × (7.4–)7.8–10 μm ($\bar{x}$ = 9.9 ± 0.9 × 8.9 ± 0.7 μm), Q = 1.04–1.2(–1.22) ($\bar{Q}$ = 1.11 ± 0.06), subglobose, broadly ellipsoid or broadly amygdaliform, echinulate; echinulae 0.3–1.5 μm long, crowded; hilar appendix 1.3–2.5 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–13 μm diam., hyaline, light yellowish brown in mass; cells barrel-shaped.

COMMENTARY—This taxon is treated as a synonym of *L. fraterna* but see Observations under *L. fraterna.*

Clitocybe tortilis var. **gracilis** Peck, Annual Rep. New York State Bot. 67: 36. 1903. Figure 64b.

TYPE: USA, New York, Bronx, N.Y. Bot. Garden, 13 July 1902, *Earle s.n.* (NYS!, holotype).

MACROMORPHOLOGY (*Teste* Peck, *ibid.*)—**Pileus** 3–6 lines broad, thin, convex, slightly umbilicate, becoming depressed or infundibuliform in age, irregular, striate, hygrophanous, when fresh reddish flesh color, paler when dry. **Lamellae** adnate to decurrent, distant, broad, pruinose when old and dry. **Stipe** 6–10 × 0.5 lines, glabrous, hollow.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with widely scattered, small fascicles of ± perpendicular hyphae; terminal cells of fascicular hyphae (N = 5) 39–67 × 10–13 μm, filamentous to subclavate, not rehydrating well; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, very thin, hyaline to light yellowish brown. **Lamellar trama** parallel; hyphae usually 2–8 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 37–60 × 8–14 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 33–55 × 2.5–4 μm, filamentous or subcapitate, abundant, thin-walled, hyaline. **Basidiospores** (excluding ornamentation) (N = 30)

(7.8–)8.3–10.6 × 7.8–10(–10.6) μm ($\bar{x}$ = 9.3 ± 0.7 × 9.1 ± 0.7 μm), Q = 1–1.06(–1.11) ($\bar{Q}$ = 1.02 ± 0.03), globose, occasionally subglobose, hyaline, echinulate; echinulae 1.4–2.3(–2.8) μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–8.5 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

COMMENTARY—The type variety has much larger basidiospores and 2-sterigmate basidia. This taxon is treated as a synonym of *L. ohiensis*, not as a variety of *L. tortilis*.

Clitocybe gruberi Smith, Mycologia 36: 245–246. 1944.

TYPE: USA, Idaho, Juliet, May 1943, *W. B. Gruber 26* (MICH!, holotype).

COMMENTARY—Singer (1949) placed this taxon in *Laccaria*. Micromorphological analysis of this collection, however, revealed the presence of very elongate, smooth basidiospores. I agree with Bigelow and Smith (1973), therefore, that this collection does not belong in *Laccaria* but belongs in the monotypic genus *Cantharocybe* Bigelow and Smith.

Agaricus grumatus Scopoli, Flora Carniolica. p. 433. 1772.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Scopoli, *ibid.*)—**Pileus** convex, dry, filamentous. *Lamellae* free, abundant. **Stipe** long, glabrous, hollow.

COMMENTARY—Fries (1836–1838) stated that this taxon showed affinities to *A. pachyphyllus* Fries, which showed affinities to *A. laccatus*. Both of these taxa are treated as synonyms of *L. laccata*.

Agaricus (Clitocybe) holoporphyrus Berkeley & Curtis, J. Linn. Soc., Bot. 10: 284. 1868.

TYPE: Cuba, *Wright no. 12* (K!, holotype).

COMMENTARY—The original description stated that the basidiospores are oblong and not subglobose as in *C. laccata*. Micromorphological analysis of this collection revealed the presence of subfusiform, smooth basidiospores. Basidiospore shape and lack of ornamentation indicate that this collection is clearly not a *Laccaria*.

Laccaria impolita Vellinga & G. M. Mueller *in* Mueller and Vellinga, Mycotaxon 37: 387–388. 1990.

TYPE: (CAG, holotype).

MACROMORPHOLOGY (*Teste* Ballero & Contu, 1989)—**Pileus** 10–40 mm diam., fleshy, convex, depressed, umbilicate, dry, squamulose-areolate at disc, elsewhere tomentose, not striate, reddish tawny to rose tawny, then ochraceous; margin involute. **Lamellae** adnate to decurrent, distant, thick, entire to slightly denticulate, concolorous with pileus. **Stipe** 40–60 × 5–8 mm, cylindric to subclavate, rarely subradicate, usually thinner at apex, fibrillose striate, concolorous; basal mycelium white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Teste* Ballero & Contu, 1989)—**Pileipellis** a trichoderm or subpalisade; hyphae clavate, pigment(s) vacuolate or membranous. **Lamellar trama** regular. **Basidia** bisterigmate. **Pleurocystidia** none. **Cheilocystidia** filamentous or subclavate. **Basidiospores** 8–12 μm diam., globose, hyaline, inamyloid; echinulae 1.3–1.8(–2) μm high, conic, distant. **Clamp connections** numerous.

COMMENTARY—Mueller and Vellinga (1990) proposed this epithet for the taxon described by Ballero and Contu (1989) as *L. singeri* (*non L. singeri* M. V. Locquin & B. M. Sarwal). According to Ballero and Contu (1989), this taxon can be differentiated from *L. fraterna* by the more robust stature, squamulose-areolate, astriate pilei, fibrillose-striate stipe, more coarsely echinulate basidiospores, arrangement of the pileipellis hyphae, and association with north temperate trees.

Agaricus (Clitocybe) incongruus Berkeley, J. Bot. (Hooker) 2: 48. 1850.

TYPE: Jillapahar, Darjeeling. Aug.-Sept., *Berkeley s.n.* (K!, holotype).

MACROMORPHOLOGY (*Teste* Berkeley, *ibid.*)—**Pileus** 31 mm broad, umbilicate, smooth, dry, cinereous-blue; margin undulate; context white. **Lamellae** 150 × 12 mm, subclavate, slightly fibrillose, hollow, concolorous with pileus.

COMMENTARY—The type collection consists of a single stipe with an attached fragment of the pileus. Virtually no hymenial material was available for micromorphological analysis, and the protologue does not include micromorphological data. Only a few basidiospores were found in the examined slides mounts, and these were nodulose, not echinulate. Although Berkeley (1850) considered it "[a] very curious species, resembling somewhat the amethyst form of *A. laccatus*, and perhaps as nearly allied to that species as to any described," it is not a *Laccaria* and probably belongs in the Entolomataceae.

Laccaria laccata var. **intermedia** Singer, Pl. Syst. Evol. 126: 368–369. 1977. Figure 64c.

TYPE: Czechoslovakia, Moravia, Jeseniky, Reiviz pr. Jesenik, 24 July 1974, *Singer C5664* (F!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 10–24 mm broad, convex, soon becoming plane to centrally depressed, when fresh glabrous or subglabrous, fibrous to filamentous when dried, strongly hygrophanous, red-brown, flesh-colored, or pallid (e.g., 11 B 6 to 11 C 6, M&P); disc subtomentose to tomentose, darker red-brown or more sordid-rose than pileus; margin translucent-striate or sulcate. **Lamellae** adnate to decurrent, subcrowded to subdistant, moderately broad, flesh-rose to dull flesh-colored. **Stipe** 30–62 × 1.8–5.8 mm, equal or thickened at base, glabrous, becoming coarse-fibered and rough, hygrophanous, concolorous with pileus or darker brown along basal half. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae (N = 10) 33–50.5 × 6–9 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel, hyphae 3–12 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** undifferentiated. **Basidia** (N = 15) 35–48.5 × 8.5–13 μm, clavate, hyaline; sterigmata (2–)4, up to 8 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 31–47 × 3–7.5 μm, filamentous to strangulate, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) (6.4–)7.4–10(–13) × (6.4–)7–10(–12.4) μm ($\bar{x}$ = 8.9 ± 1.4 × 8.6 ± 1.3 μm), Q = 0.95–1.18(–1.28) ($\bar{Q}$ = 1.04 ± 0.08), globose, subglobose, or broadly ellipsoid, hyaline, echinulate; echinulae 1.4–1.8(–2.3) μm long, not crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–14 μm diam., tightly interwoven, hyaline; cells barrel-shaped.

COMMENTARY—The basidiospore echinulae were longer than reported by Singer (1977) ("0,7–1,3 μm hoch ist, selton 1,5 μm erreicht").

This taxon is treated as a synonym of *L. laccata* var. *pallidifolia*.

Laccaria kalosperma Beeli, Bull. Soc. Roy. Bot. Belgique 66: 22. 1933.

TYPE: *Goossens 859*, Zaire, Binga, December 1929 (BR!, holotype).

COMMENTARY—Micromorphological analysis of this collection revealed the presence of strongly reticulate, amyloid basidiospores. I agree with Heinemann (1964), therefore, that this collection is a *Lactarius*, not a *Laccaria*.

Agaricus laccatus Scopoli, Flora Carniolica 2: 444. 1772. Figure 64d.

TYPE: Sweden, Femjö, 17 August 1964, *Singer 4083* (BAFC!, neotype *fide* Singer, 1967).

MACROMORPHOLOGY (*Teste* Singer, 1967)—**Pileus** (6–)15–31 mm broad, convex becoming plane, often slightly depressed, slightly striate, finely fibrillose, hygrophanous, reddish brown becoming pale ochre when dry. **Lamellae** adnate to adnate-subdecurrent, moderately distant, broad, pale, dull reddish color, white from basidiospores when dry. **Stipe** 40–60(–80) × 3–5 mm, slightly clavate, fibrous with innate fibrils, concolorous with lamellae at apex, brown toward base. **Basal mycelium** white. **Basidiospores** white in mass. **Context** concolorous with surface when moist, becoming white; odor very weak; taste sweet.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae 42–80

× 8–11 μm, filamentous, subclavate or capitate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel, hyphae 3–12 μm diam., thin-walled, hyaline; cells barrel-shaped. **Subhymenium** undifferentiated. **Basidia** 35–45 × 14–16 μm, clavate, hyaline; sterigmata 4, up to 12 μm long. **Pleurocystidia** lacking. **Cheilocystidia** 47–60 × 2.5–5 μm, filamentous, common, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) 8.7–9.2(–11) × 6.4–7.8(–8.3) μm ($\bar{x}$ = 9.2 ± 0.5 × 7.1 ± 0.5), Q = (1.11–)1.18–1.46 ($\bar{Q}$ = 1.3 ± 0.08), subglobose to ellipsoid, hyaline, echinulate; echinulae 1–1.8(–2.3) μm long, ≤ 1 μm wide at base; hilar appendix up to 2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

Russuliopsis larcina Velenovsky, Novitates Mycologicae. p. 77. 1939.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Velenovsky, *ibid.*)—**Pileus** 10 mm broad, plane, becoming depressed, glabrous, translucent-striate, dirty ochre-yellow. **Lamellae** adnate, not decurrent, crowded, narrowed at margin, white, becoming clay-colored. **Stipe** 2–3 times longer than pileus diameter, 1–1.5 mm broad, equal, straight, glabrous, translucent, fragile.

MICROMORPHOLOGY (*Teste* Velenovsky, *ibid.*)—**Basidiospores** 3–5 μm diam., globose, smooth.

COMMENTARY—Type material of this taxon was not found at either PRM or PRC. Based on the protologue, this is not a *Laccaria*.

Laccaria lateritia Malençon, Bull. Soc. Mycol. France 82: 189. 1966. Figure 65a.

TYPE: Morocco, I.S.C., *Malençon No. 5102* (Herbarium G. Malençon, holotype).

Specimen examined as representative material: Uruguay, Montevideo, 1927, *Felippone No. 2800* (MPU).

MACROMORPHOLOGY (*Teste* Malençon, *ibid.*)—**Pileus** 10–25 mm broad, thin, almost hemispherical to convex, centrally truncate or slightly depressed, becoming plane, when wet pellucid-striate to disc, not striate when dry, hygrophanous, indistinctly reddish brown to dark brick red (8, 78, 82, Klincksieck), becoming pallid. **Lamellae** mostly adnate to arcuate, moderately crowded, thick, broad, pallid rose-colored to purple-ochraceous (87 or 92, Klincksieck). **Stipe** 20–25 × 2–5 mm, thickened at base, striate, often compressed-sulcate and twisted, reddish brown, base vinaceous when immature (39, 54, 58, Klincksieck; Seguy 102, 106; Saccardo badius), lacking purple color when mature, pallid when dry. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae filamentous, subclavate or occasionally clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–10.5 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 29–46 × 8–11 μm, clavate, hyaline; sterigmata 2, up to 10 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 8.3–11(–13.3) × 8.3–10.6(–13.3) μm ($\bar{x}$ = 9.7 ± 1.04 × 9.5 ± 1.1 μm), Q = (0.95–)1–1.06(–1.11) ($\bar{Q}$ = 1.02 ± 0.03), globose, subglobose or rarely broadly ellipsoid, echinulate; echinulae 0.8–1.4 μm long, crowded; hilar appendix 1.5–2.5 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2.5–7 μm diam., narrow, morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—The micromorphological description above was based on an authentic collection on loan from Montpellier because the holotype was not available for study. Two of the four authentic collections located were not suitable. One collection was badly contaminated, and the other packet stated that it was a robust form of the taxon and, therefore, was not typical. The collection used was also somewhat contaminated, and pileipellis characters were difficult to ascertain and the presence of cheilocystidia was impossible to determine. Malençon (1966) stated that this was the first collection that he saw of this taxon.

This taxon is treated as a synonym of *L. fraterna*.

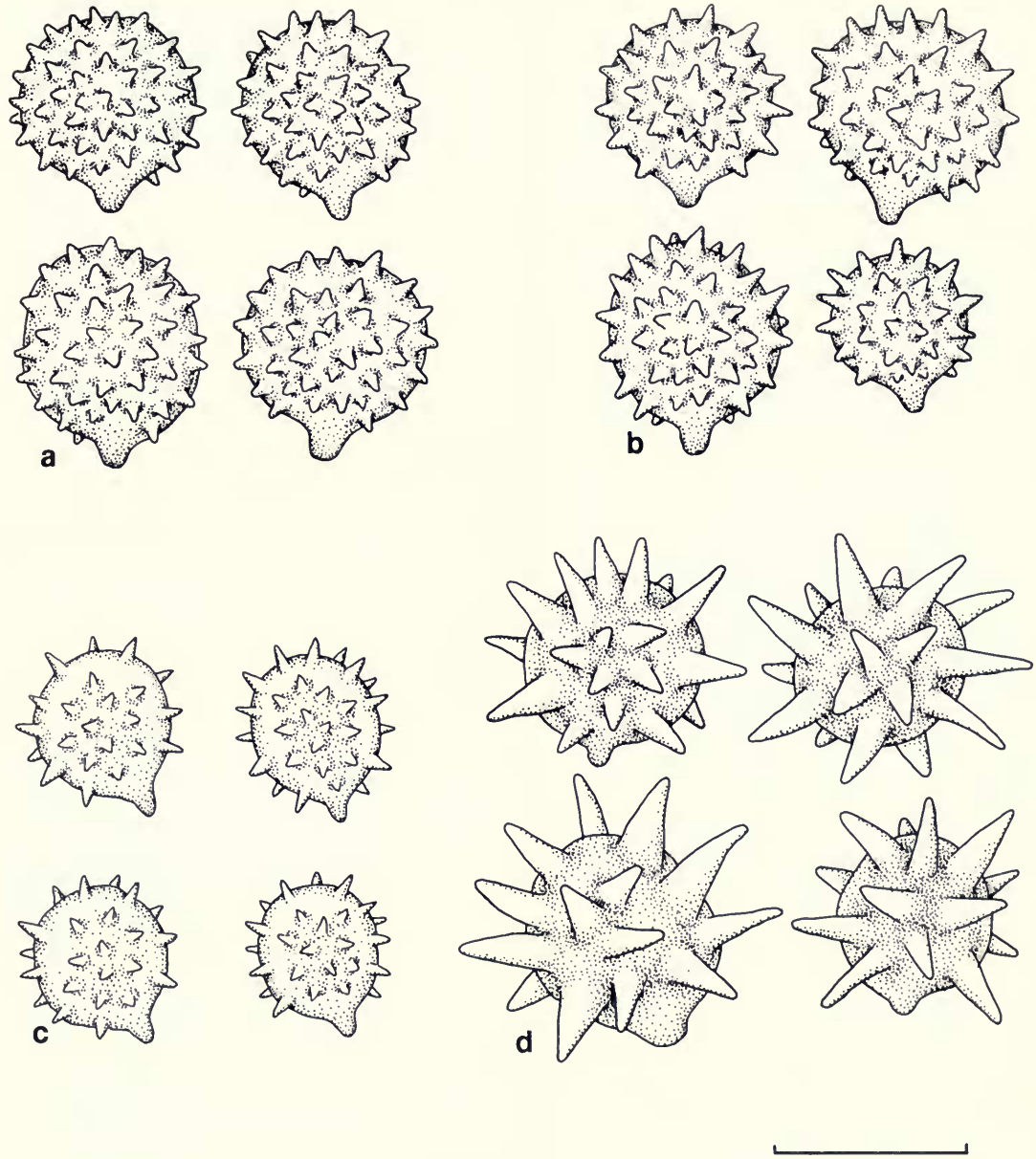


FIG. 65. Representative basidiospores from type or representative specimens: **a,** *L. lateritia* (representative specimen); **b,** *L. lilacina* (holotype); **c,** *L. longipes* (holotype); **d,** *L. masonii* (holotype). Scale line = 10 μm.

Laccaria lilacina Stevenson, Kew Bull. 19: 3. 1964. Figure 65b.

TYPE: New Zealand, Woodside, 1 July 1955, *Stevenson 924* (K!, holotype).

MACROMORPHOLOGY (*Teste* Stevenson, *ibid.*)—**Pileus** 40–55 mm broad, convex to plane, fibrillose, becoming finely scaly due to cuticular diffraction, fawn-colored with fulvous fibrils; margin upturned, often split. **Lamellae** adnate, distant, lilac, mealy. **Stipe** 100 × 30–40 mm, subfibrous, silky striate, dull fawn. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with large fascicles of ± perpen-

dicular hyphae; fascicles composed of up to 40 hyphae; terminal cells of fascicular hyphae (N = 10) 39–60 × 5–12.5 μm, filamentous to subclavate, dark yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents dark yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel; hyphae 3–9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 37–50.5 × 7–11 μm, clavate, hyaline; sterigmata 4, up to 10 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7–9.7 × 7–9.7 μm ($\bar{x}$ = 8.4 ± 0.7 × 8.3 ± 0.7 μm), Q = 1–1.07 ($\bar{Q}$ = 1.01 ± 0.03), globose, occasionally subglobose, hyaline, echinulate; echinulae (0.8–)1.4–1.8(–2.3), up to 1 μm wide at base, crowded; hilar appendix 1.3–2.5 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** 3–8 μm diam., morphologically undifferentiated, tightly interwoven, hyaline; wall up to 0.5 μm thick.

COMMENTARY—The basidiospore size and echinulae length reported here are somewhat larger than those presented in Stevenson's original description ("Sporae 7–8 μm diam., spinis 0,5–1 μm longis").

This obviously represents a distinct taxon. An examination of additional material is necessary before comments on its relationships to other taxa can be made.

Clitocybe laccata f. **lilipuntruana** Rick, Brotéria, Sér. Bot. 24: 100. 1930.

TYPE: Lacking.

COMMENTARY—No authentic material of this taxon nor a copy of the original description was located.

Russuliopsis lineata Velenovsky, Ceske Houby. p. 279. 1920.

TYPE: Housed at PRC?

MACROMORPHOLOGY (*Teste* Pilát, 1948)—**Pileus** 10–20 mm diam., obtuse to convex, becoming plane, occasionally slightly umbonate, translucent-striate, hygrophanous, honey-colored to somber brown when fresh, almost white when dry. **Lamellae** broad, thin, becoming rounded-free, farinaceous, white. **Stipe** 2–4 times longer than pileus diameter, 2–3 mm thick, equal, base not thickened, glabrous to finely fibrillose, longitudinally striate, covered with white basidiospores at apex, light gray color. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Teste* Pilát, 1948)—**Basidiospores** 8–9 μm diam., globose, thick-walled, echinulate, hyaline.

COMMENTARY—A formalin-preserved specimen of this taxon sent from PRC was never received. Without additional micromorphological data, it is impossible to clarify the concept of this taxon.

Laccaria longipes G. M. Mueller, Mycotaxon 40: 145–150. 1991. Figure 65c.

TYPE: Canada, Ontario, Nipissing District, Algonquin Provincial Park, Spruce Bog Trail, among *Sphagnum* under *Picea marinara, Larix laricina* and *Alnus rugosa,* 18 September 1984, *G. M. Mueller 1929* (F!, holotype).

MACROMORPHOLOGY (*Mihi*)—**Pileus** 11–21(–55) mm broad, convex, often centrally depressed, slightly to moderately translucent-striate, finely fibrillose, orange-brown (6B7–6C7) fading to buff in age; margin incurved, decurved, or plane, entire to undulate, becoming slightly eroded. **Lamellae** adnate, distant, thick, up to 10 mm broad, light flesh color (near 6A2). **Stipe** 67–138 × 3–8 mm, equal with slightly swollen base, dry, slightly to moderately fibrillose-striate, concolorous with pileus. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of tightly interwoven hyphae with scattered fascicles of 10–20 ± perpendicular hyphae; terminal cells 5–10 μm, filamentous to subclavate, hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline to light yellowish brown. **Lamellar trama** of parallel to subparallel hyphae, mostly 3–15 μm diam., thin-walled, hyaline; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** 28–44 × 7–12 μm, clavate, hyaline; sterigmata 4, up to 8 μm long. **Pleurocystidia** lacking. **Cheilocystidia** none seen. **Basidiospores** (excluding ornamentation) 7–8.5 × 5.7–8 μm ($\bar{x}$ = 7.7 ± 0.5 × 6.9 ± 0.6 μm), Q = 1–1.27(–1.34) ($\bar{Q}$ = 1.11 ± 0.08), subglobose to broadly ellipsoid, occasionally globose or ellip-

soid, hyaline, echinulate; echinulae (0.7–)1–1.5 (–2) μm long, less than 1 μm wide at base.

SOMATIC CULTURE MAT MORPHOLOGY: See the description under *L. longipes* in the section on North American taxa.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

Agaricus (Clitocybe) laccatus var. **lutea** Fries, Epicr. syst. mycol. p. 79. 1836–1838.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Fries, *ibid.*)—As in type variety, lamellae flesh color.

COMMENTARY—This taxon is treated as a synonym of *L. laccata.*

Agaricus (Clitocybe) laccatus var. **[pileo] luteoviolaceo** Fries, Epicr. syst. mycol. p. 79. 1836–1838.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Fries, *ibid.*)—Pileus drying ochraceous. Lamellae violaceous.

COMMENTARY—It is common for the lamellae of older specimens of *Laccaria* to turn violaceous as a result of drying or possible contamination. As this character by itself is not sufficient to warrant segregation, this taxon is treated as a synonym of *L. laccata.*

Hygrophorus maritimus Teodorowicz, Grzby wyzsze Poleskiego wybrzeza. 1936.

TYPE: Figure 5 in Teodorowicz, Grzyby wyzsze polskiego wybrzeza, Towarzystwo naukowe w Toruniu Badania Przyrodnicze Pomorskie 2: 31. 1936. (lectotype *fide* Mueller, 1991a).

MACROMORPHOLOGY (*Teste* Teodorowicz, *ibid.*)—**Pileus** 15–45 mm broad, convex becoming depressed, glabrous, appearing moist when humid, reddish flesh color; margin always unequal, toothed. **Lamellae** sinuate to arcuate, 0.5–1 mm thick, entire, reddish flesh color, drying dark brown. **Stipe** 7–35 × 6–12 mm, occasionally swollen at base, fibrillose, concolorous with pileus, apex often becoming lighter.

MICROMORPHOLOGY (*Teste* Teodorowicz, *ibid.*)—**Basidia** 25–38(–50) × 7.5–11 μm, 2–4 sterigmate. **Cystidia** lacking. **Basidiospores** 12.5–17.5 × 5.5–9 μm, ellipsoid to irregularly ovoid, hyaline to greenish, glabrous or granular.

COMMENTARY—Although no type specimen was found, the illustration and description presented in the protologue match the common usage of this name. This taxon is treated in detail in the section on North American taxa.

Laccaria masonii Stevenson, Kew Bull. 19: 4. 1964. Figure 65d.

TYPE: New Zealand, Silverstream, 19 July 1949, *Stevenson 733* (K!, holotype).

MACROMORPHOLOGY (*Teste* Stevenson, *ibid.*, McNabb, 1972)—**Pileus** 0.5–3 cm broad, convex to plano-convex when young, occasionally applanate, glabrous or minutely furfuraceous at disc, pellucid-striate at margin, hygrophanous, violaceous when young, fading to buff at maturity. **Lamellae** adnexed to adnate, distant, up to 4 mm broad, pallid violaceous when young, becoming pallid brownish pink, occasionally with faint violaceous tints remaining. **Stipe** 30–100 × 1–3 mm, swollen at base, longitudinally fibrillose-sulcate, often twisted, violaceous when young, fading to buff with maturity; apex at times with violaceous tints. **Basal mycelium** pallid violaceous. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–10 hyphae; terminal cells (N = 10) 46–67 × 8–13 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel; hyphae 2.5–6.5 diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 29.5–44 × 7.5–10.5 μm, clavate, hyaline; sterigmata 4, up to 10 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7.8–9.7(–10.6) × (7.4–)7.8–9.7(–10.6) μm ($\bar{x}$ = 8.9 ± 0.8 × 8.7 ± 0.8 μm), Q = 1–1.06(–1.11) ($\bar{Q}$ = 1.02 ± 0.03), globose to subglobose, hyaline, strongly echinulate; echinulae (1.4–)2.3–4.6(–6.5) μm long, up to 1.8 μm wide at base, occasionally curved, not crowded; hilar appendix 1.3–2.5 μm long, prom-

inent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–5.5 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

COMMENTARY—Two taxa were included in the protologue that accompanied Stevenson's original description of *L. masonii*. The type collection consists entirely of basidiocarps with glabrous pilei, and the epithet is restricted to that circumscription. McNabb (1972) proposed *L. fibrillosa* to represent the other taxon represented in the description.

Clitocybe (Lacaria) nana var. **microspora** Lange, Flora Agaricina Danica 1: 90. 1935.

TYPE: Not located.

MACROMORPHOLOGY (*Teste* Lange, *ibid.*)—**Pileus** 8 mm broad, convex-applanate, not striate, farinaceous, ash gray; disc somewhat darker. **Lamellae** attenuated behind, distant, narrow, thin, white. **Stipe** short, thin, pale ash gray. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Teste* Lange, *ibid.*)—**Pileipellis** of conidiform, lanceolate, ellipsoid cells; cells 12 × 5 μm. **Basidia** (2–)4-sterigmate. **Cystidia** 6–12 μm broad, awl-shaped or conical. **Basidiospores** 5 μm diam., subglobose, warty spinulose.

COMMENTARY—No specimen of this taxon was acquired from C. Lange (1935) stated that this taxon is a "very strange little Agaric" and that it required further study. Based on the original description, it is not a *Laccaria*.

Laccaria laccata f. **minuta** Imai, J. Fac. Sci. Hokkaido Imp. Univ., Ser. 5, Bot. 18: 90. 1938. Figure 66a.

TYPE: Japan, Prov. Ishikari, Nopporo Forest, 17 July 1932, *Imai 314* (SAP!, holotype).

MACROMORPHOLOGY (*Teste* Imai, *ibid.*)—**Pileus** 5–10 mm broad, not striate or only slightly striate. **Stipe** 25–35 × 1–2 mm, subclavate. All other characters as in the type variety.

MICROMORPHOLOGY (*Mihi*)—**Lamellar trama** parallel; hyphae mostly 5–13 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 30–43 × 9–11.5 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7–8.7(–9.2) × 7–8.7 μm ($\bar{x}$ = 8 ± 0.6 × 7.9 ± 0.6 μm), Q = 1–1.06 ($\bar{Q}$ = 1.01 ± 0.02), globose, rarely subglobose, hyaline, echinulate; echinulae 1–1.8 μm long, moderately crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–9 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—This taxon is treated as a synonym of *L. laccata* var. *pallidifolia*.

Laccaria laccata var. **moelleri** Singer, Sydowia 7: 9–10. 1973. Figure 66b.

TYPE: CSSR, Trebon, 30 September 1970, *Singer C5227* (F!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 30–69 mm broad, convex, deeply depressed, minutely fibrillose-scabrous, rusty-orange-tawny ("ferrugineo-aurantiaco-fulvo," Singer) or tawny-reddish ("fulvido-rufo," Singer), drying paler at disc; depression frequently minutely papillate; margin sulcate, rarely plicate or lobate. **Lamellae** arcuate or adnate, subcrowded to subdistant, 6–8 mm broad, rose flesh-colored ("carneorosellis," Singer) becoming covered with a white powder (?spores). **Stipe** 100–155 × 5–6(–11) mm; equal or tapering toward apex; apex finally fibrillose, becoming glabrescent, stuffed, becoming hollow, dull yellowish brown ("fulva-brunneo," Singer) or brownish ("brunneo," Singer). **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles usually composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 40–76 × 6.5–16 μm, filamentous to swollen, subclavate to clavate to ventricose-rostrate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 34–47 × 9.5–13 μm, clavate, hyaline; sterigmata 4, up to 6 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 31–57.5 × 2.5–4(–8.5) μm, filamentous, abundant, hyaline. **Basidiospores** (excluding ornamen-

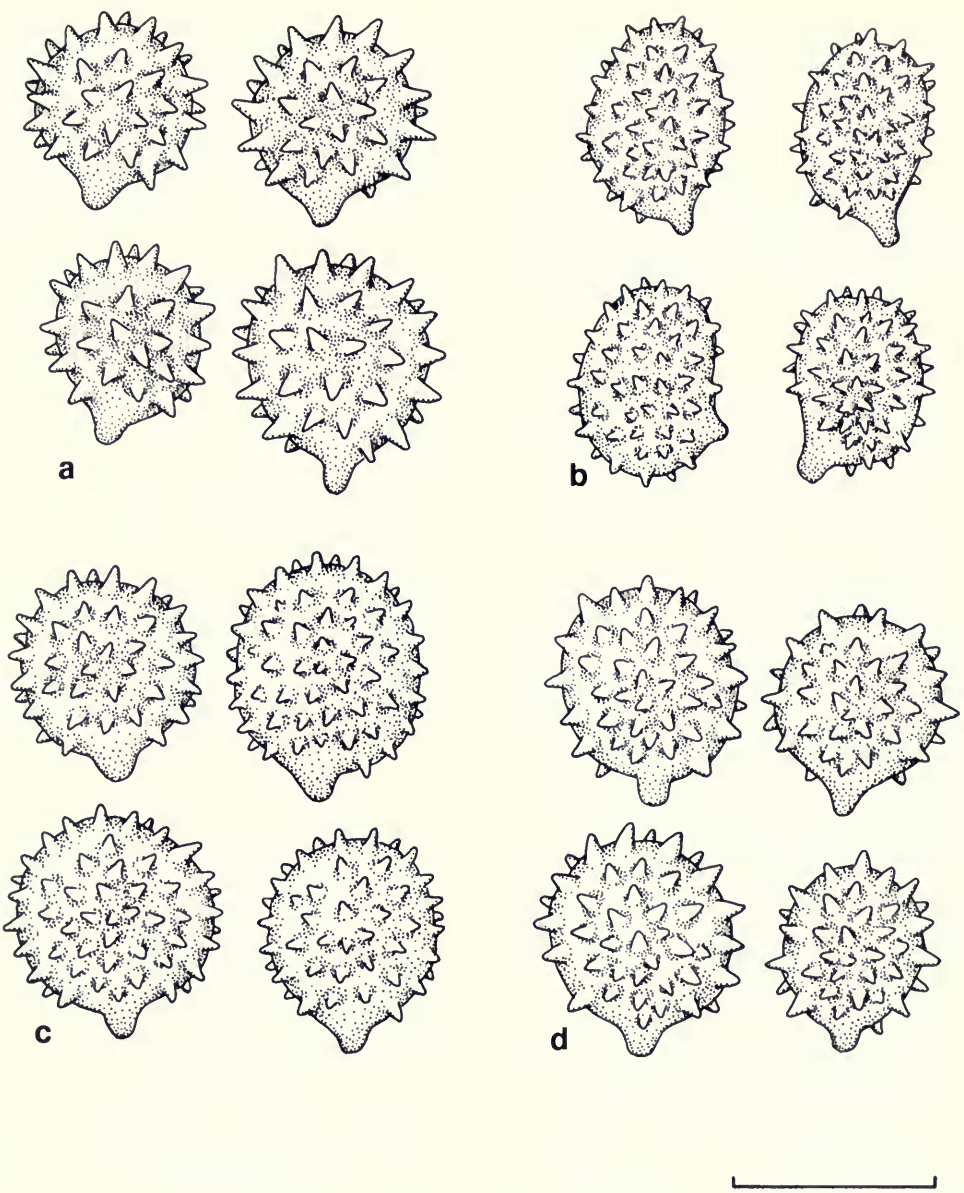


FIG. 66. Representative basidiospores from type specimens: **a,** *L. laccata* var. *minuta* (holotype); **b,** *L. laccata* var. *moelleri* (holotype); **c,** *L. laccata* var. *montana* (holotype); **d,** *L. montana* (holotype). Scale line = 10 μm.

tation) (N = 30) 9.2–11 × (6.4–)7–8.3 μm ($\bar{x}$ = 10 ± 0.6 × 7.3 ± 0.4 μm), Q = 1.24–1.46(–1.58) ($\bar{Q}$ = 1.3 ± 0.01), ellipsoid to amygdaliform, hyaline, echinulate; echinulae 0.3–1.4(–2) μm long, crowded, often with one or two long echinulae at apex; hilar appendix 1.5–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–5 μm diam., narrow, morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—Although basidiospore shape and echinulae length fit the original circumscription, the basidiospore dimensions measured in this study were all larger than the range presented by Singer.

For more information on this taxon, see Mueller

(1991a) and the discussion under *L. longipes* in the section on North American taxa.

Laccaria laccata var. **montana** Möller, Fungi of the Faeröes. pp. 269–270. 1945. Figure 66c.

TYPE: Denmark, Faeröe Ils. Ostero, Slattaratinde, 17 July 1938, *Möller s.n.* (C!, holotype).

MACROMORPHOLOGY (*Teste* Möller, *ibid.*)—**Pileus** 7–17 mm broad, convex becoming expanded, depressed in age, occasionally with a small papilla, often somewhat irregular, slightly squamulose, hygrophanous, greasy-shiny, deep flesh-colored to pallid brownish purple when fresh, fading to opaque; margin incurved at first. **Lamellae** decurrent, subdistant, thick, up to 2 mm broad, emarginate, pale pinkish flesh-colored, becoming white-mealy. **Stipe** 10–30 × 1–3 mm, equal or thickened below, straight or flexuous and twisted, fibrillose striate, hollow, concolorous with lamellae. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Lamellar trama** parallel; hyphae thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 10) 34.5–45 × 10.5–15 μm, clavate, hyaline, not rehydrating well; sterigmata 4, up to 9 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 8.3–11.5 × (7.8–)8.3–10.6 μm ($\bar{x}$ = 10 ± 0.9 × 9.6 ± 0.9 μm), Q = 1–1.11(–1.22) ($\bar{Q}$ = 1.04 ± 0.06), globose to subglobose, rarely broadly ellipsoid, hyaline, echinulate; echinulae 0.3–1.4 μm long, crowded; hilar appendix 1.5–1.8 μm long, prominent, truncate; plage present, contents occasionally uniguttulate.

COMMENTARY—The type collection consists solely of lamellar fragments contaminated by a mold. No observations could be made on the arrangement of pileipellis hyphae or stipe characteristics.

This taxon is treated as a synonym of *L. montana* Singer.

Laccaria montana Singer, Sydowia 7: 8–9. 1973. Figure 66d.

TYPE: Switzerland, Valais, Borgne de Ferpecle, 11 July 1971, *Singer M5464* (F!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 7–35 mm broad, convex, occasionally papillate when young, becoming strongly umbilicate to infundibuliform; disc rimulose to finely fibrillose, becoming diffracted to squamulose, hygrophanous or subhygrophanous, orange-brown (6 E 12 to 4 B 10 or 7 J 12 to 7 L 12, M&P) fading to ochraceous (11 F 7, M&P); margin radially sulcate. **Lamellae** adnate to decurrent, occasionally anastomosing, subcrowded to distant, broad, rose flesh-colored (11 A 8, M&P), becoming cinnamon flesh-colored (5 D 10 to 5 F 11, M&P), when dry, margin purplish brown, white pulverulent with spores. **Stipe** 15–20(–55) × 2–5 mm, equal, glabrous or innately fibrillose, more pallid than pileus to subochraceous, frequently variegated (6 B 12 and 14 A 11, M&P). **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae (N = 10) 39–51 × 5.5–10 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel; hyphae 3–14 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 42–48 × 10–15.5 μm, clavate, hyaline; sterigmata 4, up to 11 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7.8–)8.7–10.6(–11.5) × (7–)7.8–10.6 μm ($\bar{x}$ = 9.5 ± 0.8 × 8.9 ± 0.8 μm), Q = 1.0–1.11 (–1.26) ($\bar{Q}$ = 1.06 ± 0.06), globose to subglobose, hyaline, echinulate; echinulae 1.5–1.8 μm long, not crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** 3–20.5 μm diam., tightly interwoven, hyaline; cells short, barrel-shaped.

COMMENTARY—Singer (1973) reported occasional cheilocystidia ("cheilocystidiis 17–47.5 × 5.5–9.5 μm, versiformibus, clavatis, ventricose, cylindraceis vel flexuosis, frequenter pedicelliatis, hyalinis vel rubenscentibus, sat numerous"). The discrepancy between Singer's descriptions and this study may be due either to poor rehydration of the specimens or to the absence of cheilocystidia in the slide preparations examined.

This taxon is treated in detail in the section on North American taxa.

Laccaria murina Imai, J. Fac. Sci. Hokkaido Imp. Univ., Ser. 5, Bot. 18: 91. 1938.

TYPE: Not located.

MACROMORPHOLOGY (*Teste* Imai, *ibid.*)—**Pileus** 10–15 mm broad, hemispherical to convex, becoming plane, subvelutinous, striate, dark, dirty brown, almost black when young and fresh, mouse gray or subavellaneous when dry; margin involuted at first. **Lamellae** adnate, distant, gray, becoming pruinose with white spores. **Stipe** 15–25 × 1.5–2.5 mm, equal or tapering slightly above, striate, subconcolorous or slightly more pallid. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Teste* Imai, *ibid.*)—**Basidiospores** 7.5–10 μm, globose, verruculose.

COMMENTARY—No specimen of this taxon was included with the material loaned from SAP, and therefore I cannot comment on the appropriate disposition of this taxon.

Laccaria nana Massee, Kew Bull. 6: 2. 1913. Figure 67a.

TYPE: England, Grounds of Royal Botanic Gardens, Kew, Surrey, *Massee s.n.* (K!, holotype).

MACROMORPHOLOGY (*Teste* Massee, *ibid.*)—**Pileus** 10 mm broad, plano-convex, glabrous, smooth, dark cinnamon-colored, becoming pallid; margin at first farinaceous. **Lamellae** attenuate-adnate, subdistant, pallid, becoming covered with a white powder. **Stipe** 10 mm long, fibrillose, hollow, white.

MICROMORPHOLOGY (*Mihi*)—**Lamellar trama** parallel; hyphae thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** not rehydrating, ?clavate, hyaline; sterigmata 2. **Pleurocystidia** ?lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 10.6–13(–13.8) × 10.6–13(–13.8) μm ($\bar{x}$ = 11.7 ± 0.9 × 11.5 ± 0.9 μm), Q = 1–1.04(–1.09) ($\bar{Q}$ = 1.01 ± 0.03), globose, rarely subglobose, hyaline, strongly echinulate; echinulae (2.3–)2.8–4 μm long, 1.8–2.3 μm wide at base, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents usually uniguttulate.

COMMENTARY—The type collection consists of a few small lamellar fragments that contain numerous basidiospores.

This taxon appears to be a distinct species, apparently known only from the type collection. As it was collected on the grounds of Kew Gardens, it is not known whether it is native to England or was introduced.

Laccaria nigra Hongo, Mem. Shiga. Univ. 9: 58–59. 1959. Figure 67b.

TYPE: Japan, Omi-Jingu, Otsu, Shiga, 10 June 1958, *Hongo 1779* (Herbarium Hongo!, holotype).

MACROMORPHOLOGY (*Teste* Hongo, *ibid.*)—**Pileus** 8–22 mm broad, obtuse, conic to convex, becoming expanded, often with large umbo, glabrous, pellucid-striate, hygrophanous, grayish-subfuscus, disc almost black; flesh thin, membranous, concolorous, with an alkaline odor. **Lamellae** adnexed to adnate, distant, moderately thick, 1–3 mm broad, ventricose, ash gray. **Stipe** 18–35 × 1.5–3 mm, equal, hollow, concolorous with pileus.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae filamentous, subclavate or clavate, not rehydrating well; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline to light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3.5–11 μm diam., thin-walled, hyaline; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 28.5–41 × 10–15.5 μm, clavate, hyaline, not rehydrating well; sterigmata 2(–4), up to 10 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7.8–)8.3–10.6(–12.4) × (7.8–)8.3–10.6(–12.4) μm ($\bar{x}$ = 9.5 ± 1.04 × 9.5 ± 1.05 μm), Q = 1(–1.06) ($\bar{Q}$ = 1 ± 0.01), globose, rarely subglobose, hyaline, echinulate; echinulae 1.8–2.8(–3.2) μm long, 1.3–1.8 μm wide at base, moderately crowded; hilar appendix 1.5–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae**

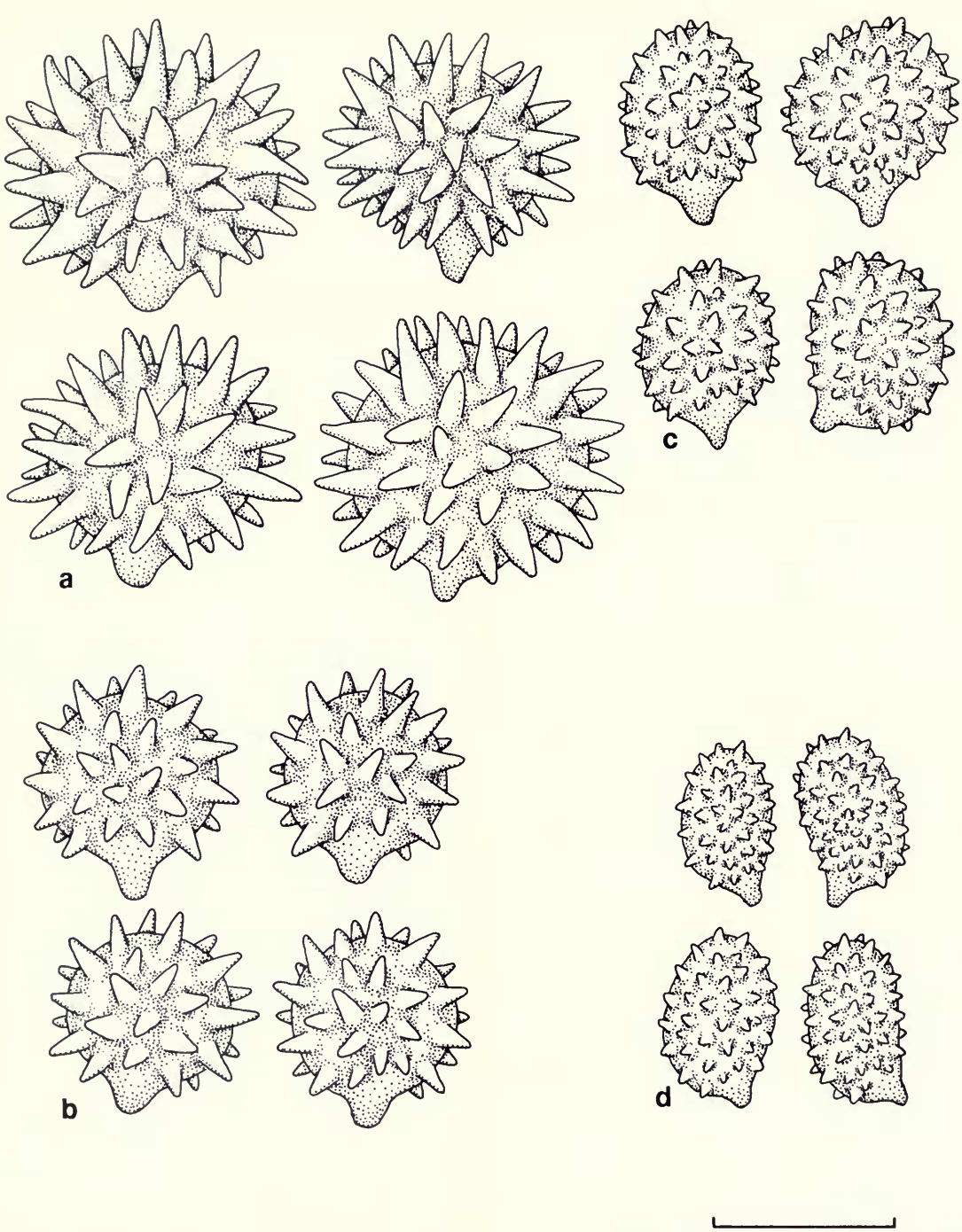


FIG. 67. Representative basidiospores from type specimens: **a,** *L. nana* (holotype); **b,** *L. nigra* (holotype); **c,** *L. nobilis* (holotype); **d,** *L. oblongospora* (holotype). Scale line = 10 μm.

mostly 3–11 μm diam., long-celled, morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—*Laccaria nigra* is obviously distinct as no other *Laccaria* has the coloration attributed to specimens of this taxon. Its affinities with other members of the genus are unclear.

Russuliopsis nigricans Velenovsky, Novitates Mycologicae. p. 77. 1939.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Velenovsky, *ibid.*)—**Pileus** 10–15 mm, bell-shaped, translucent-striate, hygrophanous, dark brown (almost black), becoming pale yellow. **Lamellae** adnate becoming sinuate to free, moderately distant, broad, thick, pale, farinose. **Stipe** 3 times longer than pileus diam., 2 mm broad, equal, straight, concolorous.

MICROMORPHOLOGY (*Teste* Velenovsky, *ibid.*)—**Basidiospores** 6–8 μm diam., globose, echinulate.

COMMENTARY—Type material of this taxon was not found at either PRM or PRC. Its affinities with other *Laccaria* are unclear.

Laccaria nobilis Smith *apud* G. M. Mueller, Mycotaxon 20: 105–108. 1984. Figure 67c.

TYPE: USA, Colorado, Larimer Co., Roosevelt National Forest, Rayah Wilderness, Blue Lake Trail, 13 September 1981, *G. M. Mueller 1198* (TENN 42527) (TENN!, holotype).

MACROMORPHOLOGY (*Mihi*)—**Pileus** 30–60 mm broad ($\bar{x}$ = 43.3 mm), convex, deeply depressed, not striate, fibrillose-scaly to scaly, brownish orange ("Sanford's Brown" to "Cinnamon-Rufous"), occasionally darker at disc ("Hazel"); margin decurved to upturned, entire to eroded. **Lamellae** sinuate to adnate, close, thick, broad, pinkish flesh color ("Pale Flesh Color" to "Flesh Color"). **Stipe** 37–110 × 4–10 mm ($\bar{x}$ = 79.5 × 6.5 mm), equal or bulbous, dry, fibrillose, fibrils forming prominent longitudinal striations, scaly from apex to midstipe, concolorous with pileus. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 20–30 hyphae; terminal cells of fascicular hyphae (N = 10) 36–58 × 7–13 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 4–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 37.5–55 × 8–11 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7.8–9.7(–10.6) × (5–)6.4–7.8(–8.3) μm ($\bar{x}$ = 8.6 ± 0.7 × 7.0 ± 0.6 μm), Q = (1.06–)1.13–1.26(–1.9) ($\bar{Q}$ = 1.23 ± 0.14), broadly ellipsoid, ellipsoid or amygdaliform, rarely subglobose or oblong, hyaline, echinulate; echinulae 0.5–1(–1.5) μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–5.5 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.

SOMATIC CULTURE MAT MORPHOLOGY—**PDA: Radius** at week 3 = 23–31 mm, week 6 = 35–42 mm; **mat** felty, thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, not translucent, at first bright violet, fading by week 6 to a dark purple band (< 9 mm) near margin with rest of mat light orange-brown; pruinose aerial hyphae light grayish purple, becoming light orange-brown; **margin** 3–4 mm broad, subfelty, thin, uneven, light violet; **plug** concolorous with mat; **hyphae** mostly undifferentiated or occasionally irregularly swollen, purplish brown in mass. **MMN: Radius** at week 3 = 40–44 mm, week 6 = 69–78 mm; mat subfelty, thin, becoming slightly thicker with age, tightly interwoven, tightly appressed to agar surface, subtranslucent, light violet; **margin** 3–4 mm broad, silky to subfelty, thin, parallel to loosely interwoven, entire, concolorous; **plug** concolorous; **hyphae** morphologically undifferentiated or rarely irregularly swollen near margin. **MEA: Radius** at week 3 = 33–35 mm, week 6 = 47–55 mm; **mat** subfelty, thin, loosely interwoven, tightly appressed to agar surface, translucent, white; **margin** 1–2 mm broad, subfelty, thinner than mat, undulate, white; **plug** white; **hyphae** morphologically undifferentiated.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

Laccaria oblongospora G. M. Mueller, Mycotaxon 20: 108–112. 1984. Figure 67d.

TYPE: USA, Mississippi, Harrison Co., DeSoto National Forest, Harrison Experimental Forest, Road H-8, 7 December 1980, *G. M. Mueller 1102* (TENN 42522) (TENN!, holotype).

MACROMORPHOLOGY (*Mihi*)—**Pileus** 14–54 mm broad ($\bar{x}$ = 29 mm), convex becoming plane, often depressed, not striate, finely fibrillose, becoming fibrillose-scaly, hygrophanous, brownish orange ("Cinnamon-Rufous," "Hazel," or "Sanford's Brown"), occasionally darker at disc ("Chocolate"); margin decurved to upturned, entire to undulate, becoming eroded; context 1–2 mm thick, tapering quickly to margin, flesh-colored ("Pale Vinaceous-Pink"). **Lamellae** sinuate to adnate, subdistant to distant, thick, broad, pinkish flesh color ("Shell Pink," Vinaceous-Pink," or near "Buff-pink"). **Stipe** 23–60 × 3–10 mm ($\bar{x}$ = 41 × 5 mm), equal or bulbous, dry, fibrillose, occasionally finely longitudinally-striate, brownish orange to reddish brown ("Pinkish Cinnamon," "Cinnamon," or "Cacao Brown"), occasionally with darker fibrils ("Pecan Brown"). **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of loosely interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–15 hyphae; terminal cells of fascicular hyphae (N = 10) 28.5–69 × 13–25 μm, subclavate, clavate, or capitate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel; hyphae thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 10) 29–36 × 7.5–10 μm, clavate, hyaline; sterigmata 4, up to 5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 31.5–53 × 2.5–7 μm, filamentous to subclavate, scattered, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) (6.8–)7.4–9.2(–10) × (4–)5–6.4(–7) μm ($\bar{x}$ = 8.4 ± 0.8 × 5.8 ± 0.5 μm), Q = (1.25–)1.3–1.67(–1.8) ($\bar{Q}$ = 1.46 ± 0.13), ellipsoid to oblong, occasionally subreniform, hyaline, echinulate; echinulae < 0.5 μm long, often with 1 or 2 longer spines (≤ 1.4 μm) at apex, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–11 μm diam., tightly interwoven, hyaline; cells barrel-shaped.

SOMATIC CULTURE MAT MORPHOLOGY—**PDA: Radius** at week 3 = 31–36 mm, week 6 = 70–75 mm; **mat** felty, moderately thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, not translucent, at first dark violet, then fading; week 3 moderate violet 2–3 mm band near margin, most of mat light orange-brown, week 6 entirely light orange-brown; margin up to 5 mm broad, silky to subfelty, thin, uneven, light violet to white; **plug** concolorous with mat; **hyphae** mostly morphologically undifferentiated, occasionally irregularly swollen or subcoralloid. **MMN: Radius** at week 3 = 52–56 mm, week 6 = > 100 mm (plate full); **mat** subfelty to subwoolly, thin, loosely interwoven, tightly appressed to agar surface, translucent, initially light violet, fading to white; **margin** undifferentiated, uneven; **plug** concolorous with mat; **hyphae** mostly morphologically undifferentiated, occasionally irregularly swollen. **MEA: Radius** at week 3 = 26–31 mm, week 6 = 54–60 mm; **mat** subfelty, thin, loosely interwoven, tightly appressed to agar surface, translucent, white; **margin** 1–2 mm broad, not well differentiated, even, white; **plug** white.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

Agaricus (Clitocybe) ochropurpureus Berkeley, London J. Bot. 4: 299–300. 1845. Figure 68a.

TYPE: USA, Ohio, Cincinnati, no date, *Lea 261* (K!, holotype).

MACROMORPHOLOGY (*Teste* Berkeley, *ibid.*)—**Pileus** 50 mm broad, subhemispherical becoming depressed, fleshy pliant, pale brown to light purple; cuticle easily separating; margin incurved; at first tomentose. **Lamellae** decurrent, thick, not anastomosing, purple. **Stipe** 60 mm, swollen at middle, pallid purple. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Lamellar trama** parallel; hyphae 3–7 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 3) 36–45 × 9–10.5 μm, clavate, hyaline, not rehydrating well, sterigmata 4, up to 6 μm long. **Pleurocystidia** not observed. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7–)7.4–8.7 × (6.4–)7–8.3(–8.7) μm ($\bar{x}$ = 8 ± 0.5 × 7.6 ± 0.6 μm), Q = 1–1.13(–1.16) ($\bar{Q}$ = 1.06 ± 0.05), globose to subglobose, hyaline, echinulate; echinulae (0.3–)1–1.4 μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate.

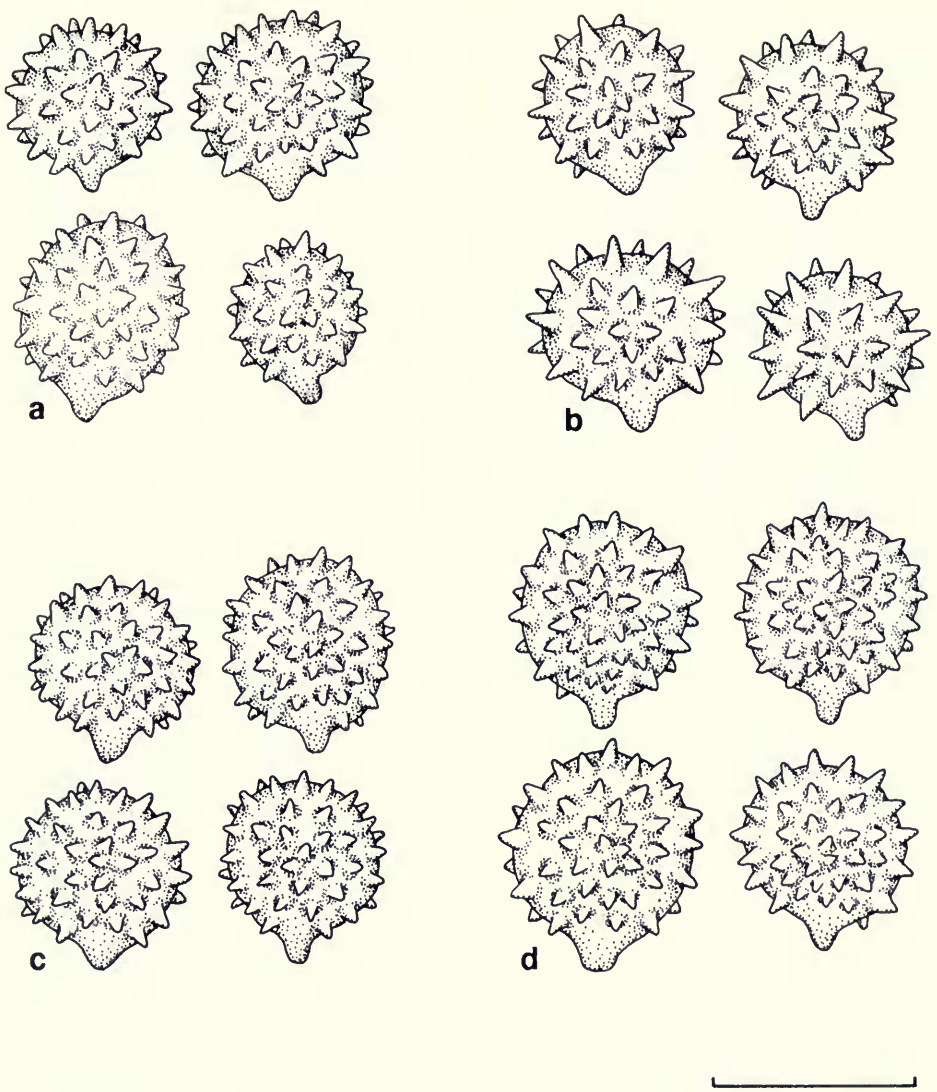


FIG. 68. Representative basidiospores from type specimens: **a,** *A. ochropurpureus* (holotype); **b,** *A. ohiensis* (holotype); **c,** *C. laccata* var. *pallidifolia* (holotype); **d,** *L. ohiensis* var. *paraphysata* (holotype). Scale line = 10 μm.

COMMENTARY—Because of the poor condition of this collection, no observations could be made on the arrangement of hyphae in the pileipellis or the presence or absence of cheilocystidia.

This taxon is treated in detail in the section on North American taxa.

Agaricus ohiensis Montagne, Syll. Crypt. p. 100. 1856. Figure 68b.

TYPE: USA, Ohio, Columbus, *Sullivant s.n.* (PC!, holotype).

MACROMORPHOLOGY (*Teste* Montagne, *ibid.*)—**Pileus** 30–50 mm broad, at first hemispherical, becoming convex, deeply depressed, glabrous, striate, cinnamon-colored; margin involuted to plane. **Lamellae** 3–5 mm broad, thick, subdistant, decurrent, rose-colored or more pallid than pileus; edge obtuse. **Stipe** 30–40 × 5–6 mm, thickened at base, striate, hollow, concolorous with pileus. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae, with scattered fascicles of ± perpendicular hyphae, not rehydrating well. **Pileus trama** tightly interwoven, morphologically undif-

ferentiated, hyaline, yellowish brown toward pileipellis. **Pileus trama** parallel, cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 30–46(–53) × 8.5–14.5 μm, clavate, not rehydrating well, hyaline, sterigmata (2–)4, up to 8.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7.4–9.2(–10) × 7.4–9.2(–10) μm ($\bar{x}$ = 8.4 ± 0.6 × 8.4 ± 0.6 μm), Q = 0.95–1.06 ($\bar{Q}$ = 1.01 ± 0.03), globose to subglobose, hyaline, echinulate; echinulae 1.4–2.3 μm long, > 1.2 μm wide at base, hilar appendix 1.8–2.3 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 1.5–3 μm diam.; tightly interwoven, morphologically undifferentiated, hyaline.

COMMENTARY—The first published report of the micromorphology of the type specimen (Singer, 1942) stated that the basidia were 4-sterigmate. In subsequent papers, however, Singer (1946, 1949, 1967, 1977, 1986), Bon (1983), and others reported that the basidia were 2-sterigmate. My observations of the holotype corroborate Lahaie's description (1981) that the basidia of the holotype of *A. ohiensis* are 4-sterigmate. A small fragment of the type collection is housed also at NY.

This taxon is treated in detail in the section on North American taxa.

Agaricus orbisporus Britzelmayr, Revis Hymenomyc. I: 15. 1898.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Saccardo, 1912)—**Pileus** 25 mm broad, conical to convex, umbonate, hygrophanous, brownish gray, becoming pale. **Lamellae** arcuate, distant, moderately thick, 4 mm broad, gray. **Stipe** 70 × 5 mm, brownish gray to white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Teste* Saccardo, 1912)—**Basidiospores** 8–10 μm diam., globose.

COMMENTARY—This taxon is putatively similar to *A. echinosporus* (Saccardo, 1912). *Agaricus orbisporus* is treated as a synonym of *L. tortilis.*

Agaricus pachophyllus Fries, Obs. Mycol. I: 76. 1815.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Fries, *ibid.*)—**Pileus** plano-convex, becoming depressed, somewhat fleshy, grayish yellow; margin becoming rimose. **Lamellae** decurrent, light yellow. **Stipe** 1.5 unc., glabrous, solid becoming hollow, yellow.

COMMENTARY—Fries (1821) listed this taxon (as "*A. pachyphyllus*") as one that needed more study. Although Fries (1836–1838) later stated that this taxon was similar to *A. laccatus,* the lamellae and stipe colors presented in the protologue make it doubtful that this taxon is a *Laccaria.*

Clitocybe laccata var. **pallidifolia** Peck, Annual Rep. New York State Bot. 43: 38. 1890. Figure 68c.

TYPE: USA, New York, Selkirk, October, *C. H. Peck s.n.* (NYS!, holotype).

MACROMORPHOLOGY (*Teste* Peck, *ibid.*)—**Lamellae** much paler than typical, with only a tinge of flesh color.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–25 hyphae; terminal cells of fascicular hyphae (N = 10) 24–53 × 6–10 μm, filamentous to clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 3–9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 39–57.5 × 10.5–15.5 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7.8–11(–11.5) × 7.4–9.2(–10.6) μm ($\bar{x}$ = 9.2 ± 0.9 × 8.5 ± 0.8 μm), Q = 1–1.12(–1.2) ($\bar{Q}$ = 1.08 ± 0.06), globose to subglobose, occasionally broadly ellipsoid, hyaline, echinulate; echinulae 0.5–1.4(–1.8) μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 5–11 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—The collection labeled TYPE on loan from NYS contained material from two localities, Selkirk and Lake Mohonk. Specimens from both locations were examined and found contaxic.

This taxon is treated in detail in the section on North American taxa.

Laccaria ohiensis var. **paraphysata** McNabb, New Zealand J. Bot. 10: 474–475. 1972. Figure 68d.

TYPE: New Zealand, Auckland, Titirangi, Atkinson Park, 12 July 1967, *McNabb PDD 25973* (PDD!, holotype).

MACROMORPHOLOGY (*Teste* McNabb, *ibid.*)—**Pileus** 10–35 mm broad, convex to plano-convex at maturity, occasionally depressed, inconspicuously translucent-striate at margin when wet, not so when dry, finely furfuraceous, hygrophanous, reddish brown to dark reddish brown, drying pallid fawn to buff. **Lamellae** adnexed to adnate, distant, thick, up to 5 mm broad, flesh pink, glaucous. **Stipe** 25–70 × 2–5 mm, equal or tapering slightly apically, dry, coarsely and sparingly longitudinally fibrillose, often twisted, reddish brown. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 32–64 × 6.5–10.5 μm, filamentous, swollen, subclavate or clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel; hyphae 3.5–11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 33–50.5 × 8.5–12 μm, clavate, hyaline; sterigmata 2(3), up to 11 μm long. **Pleurocystidia** (N = 10) 27–42 × 2.5–4.5 μm, filamentous, subclavate, subcapitate or irregularly contorted, sometimes irregularly branched, thin-walled, hyaline. **Cheilocystidia** 20–41.5 × 1.8–3 μm, similar to pleurocystidia. **Basidiospores** (excluding ornamentation) (7.4–)7.8–9.7(–11.5) × 7.4–9.7(–11.5) μm ($\bar{x}$ = 9.1 ± 0.8 × 8.9 ± 0.8 μm), Q = 1–1.05(–1.12) ($\bar{Q}$ = 1.02 ± 0.03), globose to subglobose, hyaline, echinulate; echinulae 0.8–1.4 μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2.5–9 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—As discussed in the section on North American taxa, the holotype of *Agarius ohiensis* is tetrasporic, not bisporic as had been reported. As such, this bisporic taxon cannot be a variety of *L. ohiensis* but must be renamed.

Laccaria tetraspora var. **peladae** Singer, Bull. Soc. Mycol. France 83: 117. 1967. Figure 69a.

TYPE: Chile, Valdivia, Cordillera Pelada, El Mirador, 5 May 1965, *Singer M5515* (BAFC!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—As in *L. tetraspora* var. *tetraspora*.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 37–60 × 5–13.5 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 4.5–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 32–44 × 9–12.5 μm, clavate, hyaline; sterigmata (2–)4, up to 10 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 20–34.5 × 3–4 μm, undifferentiated, thin-walled, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) (6.4–)7–9.2 × (6.4–)7–9.2 μm ($\bar{x}$ = 7.9 ± 0.7 × 7.8 ± 0.7 μm), Q = 1–1.06 ($\bar{Q}$ = 1.01 ± 0.02), globose, occasionally subglobose, hyaline, echinulate; echinulae 0.8–1.4(–1.8) μm, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 6.5–18 μm diam., tightly interwoven, hyaline, walls up to 0.5 μm thick; cells filamentous to barrel-shaped.

COMMENTARY—Singer (1967) separated *L. tetraspora* var. *peladae* from *L. tetraspora* var. *tetraspora* solely on slight differences in basidiospore and basidiospore ornamentation size. Singer (1977) later transferred this taxon to *L. laccata* var. *peladae*.

This taxon is treated as a synonym of *L. laccata* var. *pallidifolia*.

Agaricus (Clitocybe) laccatus var. **perpusillus** Rabenhorst et al., Fungi Europaei Exsiccati. Cent 5. n. 503. 1862.

TYPE: Not located.

Specimen examined as representative material: *Rabenhorst No. 503*, Fungi Europaei Exsiccati, Finland, Mustiala tradgard, September 1866 (NY).

MICROMORPHOLOGY (*Mihi*)—**Basidia** 2-sterigmate. **Basidiospores** (excluding ornamentation)

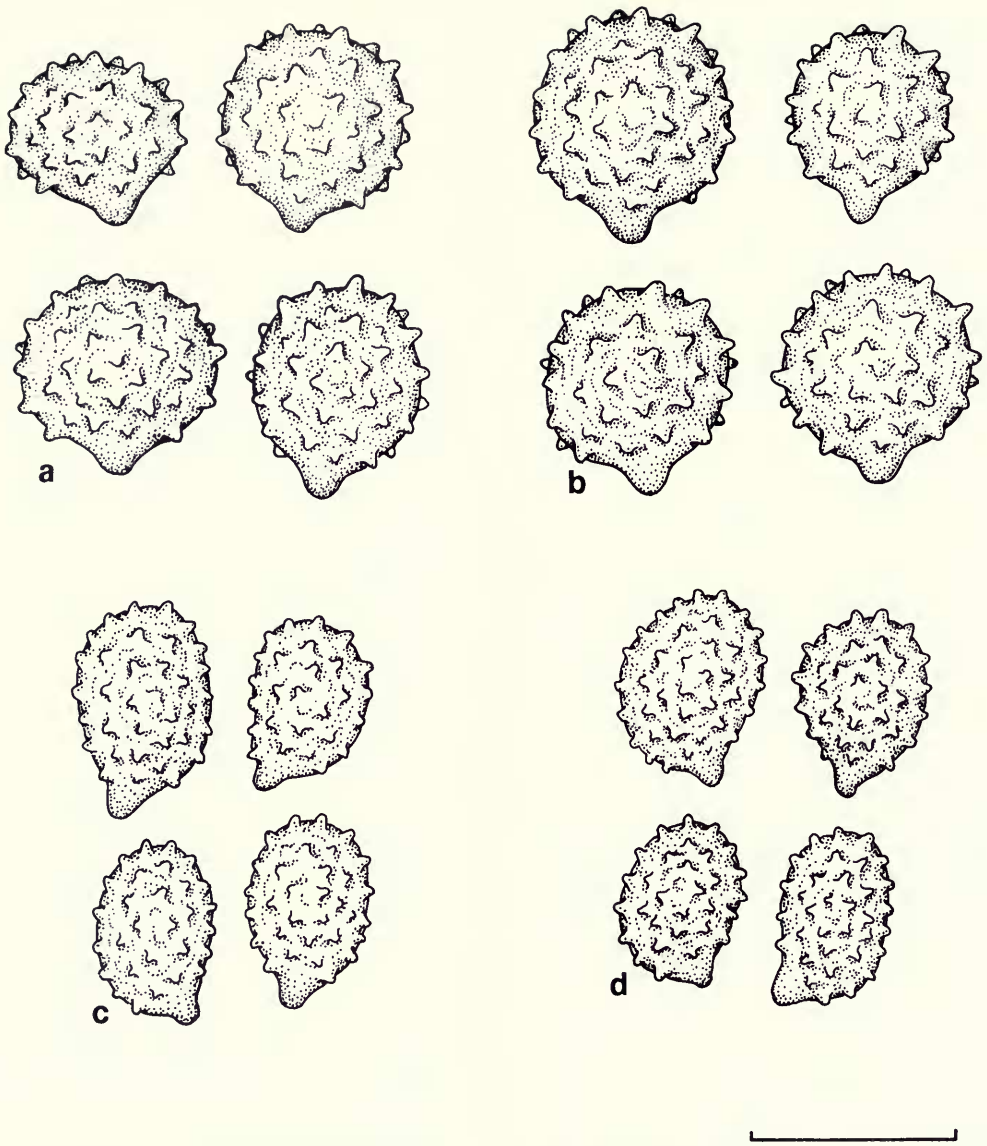


FIG. 69. Representative basidiospores from type or representative specimens: **a,** *L. tetraspora* var. *peladae* (holotype); **b,** *L. tetraspora* var. *peullensis* (holotype); **c,** *L. proxima* (representative specimen); **d,** *L. proximella* (holotype). Scale line = 10 μm.

10.5–14 μm diam., globose to subglobose, hyaline, echinulate; echinulae up to 3 μm long.

COMMENTARY—This collection consists of fragments of two pilei. Because of the date on the collection, 1866, it is doubtful that Rabenhorst had this particular collection available to him when he first designated the variety. Other specimens in the exsiccati, therefore, may be better candidates for typification.

The micromorphology of this collection fits within the circumscription of *L. tortilis* and this taxon is treated as a synonym of *L. tortilis.*

Laccaria tetraspora var. **peullensis** Singer, Bull. Soc. Mycol. France 83: 113–114. 1967. Figure 69b.

TYPE: Chile, Peulla, Lago Todos los Santos, 22 March 1959, *Singer M1991* (BAFC!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 8–10 mm broad, campanulate or conic-obtuse, glabrous, pellucid-striate, hygrophanous (13 A 8 and 14 A 9, M&P). **Lamellae** adnate, moderately broad (1 C 2 to 3 C 9, M&P). **Stipe** 50–55

× 2–3 mm, equal, slender (13 A 9 and 14 A 10, M&P). **Basal mycelium** pale, whitish when dry.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae, no fascicles of hyphae observed, terminal cells (N = 10) 28–55 × 6.5–13 μm, filamentous, clavate or ventricose; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Pileus trama** parallel; hyphae mostly 3–9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 28.5–42 × 10–16.5 μm, clavate, hyaline; sterigmata 4, up to 8.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 24–38 × 3–5.5 μm, filamentous, subcapitate or narrowly ventricose-rostrate, abundant, thin-walled, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) 7.4–8.7(–9.7) × 7.4–8.7(–9.2) μm ($\bar{x}$ = 8.1 ± 0.6 × 8 ± 0.5 μm), Q = 1(–1.11) ($\bar{Q}$ = 1.01 ± 0.02), globose, rarely subglobose, hyaline, echinulate; echinulae 1–1.8 μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–5.5 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—The collection consists of part of a single basidioma. This taxon is treated as a synonym of *L. ohiensis*.

Agaricus (Clitocybe) porphyrellus Berkeley & Curtis, Ann. Mag. Nat. Hist. III. 4: 284–285. 1859.

TYPE: USA, Connecticut, collected by C. Wright, no date, *Curtis No. 5520* (K!, holotype).

MACROMORPHOLOGY (*Teste* Berkeley & Curtis, *ibid.*)—**Pileus** 37 mm broad, convex, glabrous, pale dull purple. **Lamellae** pale purple. **Stipe** 25–37 × 2–3 mm, thickened upward, glabrous, purplish white.

MICROMORPHOLOGY (*Teste* Berkeley & Curtis, *ibid.*)—**Basidiospores** ellipsoid 1/5,750 in. long.

COMMENTARY—The original description includes little micromorphological data. Berkeley and Curtis (1859) stated that this collection "[d]iffers from *A. laccatus* in the numerous gills and very different spores." The type collection consists of one very moldy basidiocarp from which no micromorphological observations could be obtained. Murrill (1916) also reported that the specimen was in poor condition, rendering interpretation difficult. He speculated that it is "*Prunulus purus* or one of the species of *Laccaria*" (Murrill, 1916). Without micromorphological data, it is impossible to clarify the concept of this taxon, and its identity remains uncertain. No material fitting this description was found during this study.

Agaricus (Clitocybe) porphyrodes Berkeley & Broome, J. Linn. Soc. 11: 519. 1871.

TYPE: Ceylon, Peradeniya, November 1868, *Berkeley & Broome 840* (K!, holotype).

COMMENTARY—The type collection consists of a single basidioma. Micromorphological analysis of this specimen revealed the presence of globose, smooth basidiospores. Although Cooke (1884) included this epithet when he transferred names into *Laccaria* (Cooke, 1884, p. 70), the lack of echinulate or roughened basidiospores excludes it from the genus.

Clitocybe proxima Boudier, Bull. Soc. Bot. France 28: 91–92. 1881. Figure 69c.

TYPE: Plate II, fig. 2 in Boudier, Bull. Soc. Bot. France vol. 28. 1881 (lectotype *fide* Mueller, 1991a). Representative specimen: France, Montemorency, November 1904, *Boudier s.n.* (as *C. proxima*) (PC!, "neotype" *fide* Mueller, 1987).

MACROMORPHOLOGY (*Teste* Boudier, *ibid.*)—**Pileus** up to 30 mm broad, convex, becoming plane, depressed, covered with appressed fibrils, hygrophanous, orange-rust ("fauve orange," Boudier), disc becoming squamulose with age; margin striate when moist. **Lamellae** distant, thick, pinkish flesh-colored ("rose carne," Boudier), paler toward margin, becoming subconcolorous with pileus, often covered with a white powder (?spores). **Stipe** up to 40 × 4 mm long, externally fibrillose, equal or slightly thickened at base.

MICROMORPHOLOGY (*Mihi*, based on representative specimen)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae (N = 10) 38–64 × 4.5–9 μm, filamentous, subclavate, clavate, or occasionally subcapitate, light yellowish brown in mass; walls up to 0.5 μm thick, pale yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hya-

line, light yellowish brown toward pileipellis. **Pileus trama** parallel; hyphae 3.5–12 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 30.5–43 × 8.5–11.5 μm, clavate, hyaline; sterigmata 4, up to 5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7.8–11 × (6.4–)7–8.3(–8.7) μm ($\bar{x}$ = 9.6 ± 1 × 7.6 ± 0.6 μm), Q = (1.05–)1.12–1.49 ($\bar{Q}$ = 1.3 ± 0.1), ellipsoidal or amygdaliform, rarely subglobose, hyaline, echinulate; echinulae 0.5–1(–2.3) μm long, sometimes with 1 or 2 long echinulae at apex; hilar appendix, 1.5–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2.5–4 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.

COMMENTARY—Several conflicting accounts of this name have been published as a result of different interpretations of Boudier's (1881) illustration and brief description (see Mueller & Sundberg, 1981; Contu, 1986). While designating Boudier's illustration as lectotype adheres to the ICBN (Greuter et al., 1988), it does not resolve the nomenclatural and taxonomic confusion that has been associated with this epithet. To stabilize the application of this epithet, the collection originally proposed as neotype (Mueller, 1987) is designated the "representative specimen."

Although collected 23 years after the original publication date, this is the only collection of Boudier's labeled *C. proxima* at PC. Thus, it is the only authentic material from which to designate a representative specimen. Basidiospore data of this collection closely fit those in the original description ("spores ovales, finement echinulees"). Although difficult to discern with certainty owing to possible preservation artifacts, the basidiomata appear to fit the morphological criteria as well.

This taxon is treated in detail in the section on North American taxa.

Laccaria proximella Singer *in* Singer and Moser, Mycopathol. Mycol. Appl. 26: 146–147. 1965. Figure 69d.

TYPE: Chile, Valdivia, Cordillera Pelada, 30 March 1963, *Singer M3247* (BAFC!, paratype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 20–34 mm broad, convex, depressed, dry, radiately fibrillose, flesh-colored-brown ("incarnato-bruneo," Singer). **Lamellae** adnate or subsinuate, subdistant, moderately thick, broad, flesh-colored ("carneolis," Singer). **Stipe** up to 42 × 6.5 mm, equal or tapering toward apex, ± concolorous with pileus. **Basal mycelium** white. **Stipe context** flesh-colored, sordid purple toward base of stipe. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae, fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae (N = 10) 42–64 × 6.5–13 μm, filamentous, subclavate, subcapitate or capitate, light yellowish brown in mass; walls up to 0.5 μm thick, pale yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 5.5–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 23–40 × 8–14.5 μm, clavate, hyaline; sterigmata (2–)4, up to 7.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (8.3–)8.7–11 × 6–8.3 μm ($\bar{x}$ = 9.6 ± 0.7 × 7.3 ± 0.6 μm), Q = 1.18–1.46 ($\bar{Q}$ = 1.3 ± 0.1), ellipsoidal to amygdaliform, hyaline, echinulate; echinulae 0.5–1(–2.3) μm long, crowded, occasionally with one or two long echinulae at apex; hilar appendix 1.4–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** 5–25 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.

COMMENTARY—Singer and Moser (1965) reported sparse cheilocystidia ("cheilocystidiis admodum sparsis, filamentosis ± 3–3.7 μ latis, hyalinis"). The discrepancy between Singer's account and this description may be due to poor rehydration or to the absence of cheilocystidia in the slide preparations examined.

This taxon is discussed in more detail under *L. proxima* in the section on North American taxa.

Clitocybe pruinosa Lovejoy, Bot. Gaz. (Crawfordsville) 50: 383. 1910.

TYPE: USA, Wyoming, Foxpark, 14 August 1909, *Lovejoy 83* (RM, holotype).

MACROMORPHOLOGY (*Teste* Lovejoy, *ibid.*)—**Pileus** 30–50 mm broad, plano-convex, slightly depressed, dry, glabrous, shining, rich reddish

brown over salmon; margin decurved, entire, paler than pileus. **Lamellae** strongly decurrent, close, thin, salmon yellow, becoming powdered with white basidiospores. **Stipe** 50 × 10 mm, fleshy, glabrous, subconcolorous with pileus, hollow. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Teste* Lovejoy, *ibid.*)—**Basidiospores** 7–10.5 μm, globose, spiny.

COMMENTARY—No authentic material of this taxon could be found at RM, and no material referable to it was found during this study.

Laccaria laccata var. **pseudobicolor** Bon *in* Bon and Haluwijn, Doc. Mycol. 12 (46): 42. 1982. Figure 70a.

TYPE: France, Carvin, Pas-de-Calais, 21 October 1970, *M. Bon 70428* (Herb. M. Bon!, holotype).

MACROMORPHOLOGY (*Teste* Bon, *ibid.*)—**Pileus** 20–30(–35) mm broad, convex to plane, slightly depressed, slightly squamulose at disc (in the manner of *L. proxima*), fibrillose toward margin, orange-brown ("fauve orangé"); margin incurved, crenulate. **Lamellae** adnate to arcuate, relatively distant, pale rose lilac. **Stipe** (40–)50–70 × 3–4 (–5) mm, tough, slightly fibrillose, ± concolorous with pileus, paler or rose lilac at apex, vinaceous brown at base. **Context** ± concolorous or paler than pileus; odor lacking; taste bland or amarescent. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with ascending fascicles of hyphae; terminal cells of fasciculate hyphae 8–10 (–18) μm diam., with rounded apices, brownish in mass. **Pileus trama** morphologically undifferentiated. **Lamellar trama** parallel; hyphae mostly 5–18 μm diam., filamentous or barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** clavate; sterigmata 4. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (6.5–)7–8.5(–9) × (5.5–)6–7(–7.5) μm ($\bar{x}$ = 8.3 ± 0.5 × 6.9 ± 0.4 μm), Q = 1.15–1.35; broadly ellipsoid, occasionally ellipsoid or subglobose, echinulate; echinulae 1–1.5 μm long, ≤ 1 μm wide at base; hilar appendix truncate.

COMMENTARY—This taxon is treated as a synonym of *L. bicolor*.

Clitocybe puiggarii Spegazzini, Bol. Acad. Ci. (Córdoba) 11: 389. 1889.

TYPE: Brazil, Apiahy, April 1888, *Spegazzini 16080* (LPS!, holotype).

COMMENTARY—The type collection consists of part of a single poorly preserved basidioma. Although pencil drawings on the packet illustrate globose, echinulate basidiospores, all the observed basidiospores were globose to oblong, reticulate, and amyloid. I agree, therefore, with Singer's (1950b, p. 136) view that this collection is referable to *Russula*.

Clitocybe pulchella Spegazzini, Bol. Acad. Ci. (Córdoba) 11: 389–390. 1889.

TYPE: Brazil, Apiahy, June 1882, *Spegazzini 16084* (LPS!, holotype).

COMMENTARY—The type collection consists of a single, small, moldy basidioma. No basidiospores could be found, although numerous echinulate conidia were observed. Pencil sketches on the packet illustrate a typical *Laccaria*-shaped basidioma and globose basidiospores, some echinulate, others nodulose. Singer (1943a, p. 17) transferred this name to *Laccaria* but did not give the basionym. In 1950a, Singer transferred the name to *Marasmiellus*, stating that an examination of the type specimen revealed only echinulate conidia and no basidiospores. Singer (1950a, pp. 190–191) based this new combination on a comparison of the type specimen with another collection, presumed contaxic, that had oblong, smooth basidiospores.

Laccaria pumila Fayod, Ann. Della R. Acc. di Agric. di Torino 35: 91. 1893. Figure 70b.

TYPE: France, dept. Alpes maritimes, Col de la Cayolle, 2500 m alt., 18 July 1976, *J. Trimbach 1453* (L!, neotype *fide* Mueller & Vellinga, 1986).

MACROMORPHOLOGY (*Teste* Fayod, *ibid.*)—**Pileus** 5 mm broad at first, campanulate, then 10–15 mm broad, plane, centrally depressed, strongly striate, undulate, mahogany color when moist, ochraceous when dry, disc darker. **Lamellae** adnexed, submarginate, flesh color. **Stipe** 20 × 1.5 mm, slightly thickened upward, flexuous, hollow, concolorous with pileus. **Basal mycelium** cottony, white.

MICROMORPHOLOGY (*Mihi*)—**Pileus trama** parallel, hyphae 3–7 μm diam., thin-walled, hyaline; cells morphologically undifferentiated. **Subhymenium** morphologically undifferentiated. **Basidia** 32–55 × 10–15 μm, clavate, hyaline; sterigmata 2,

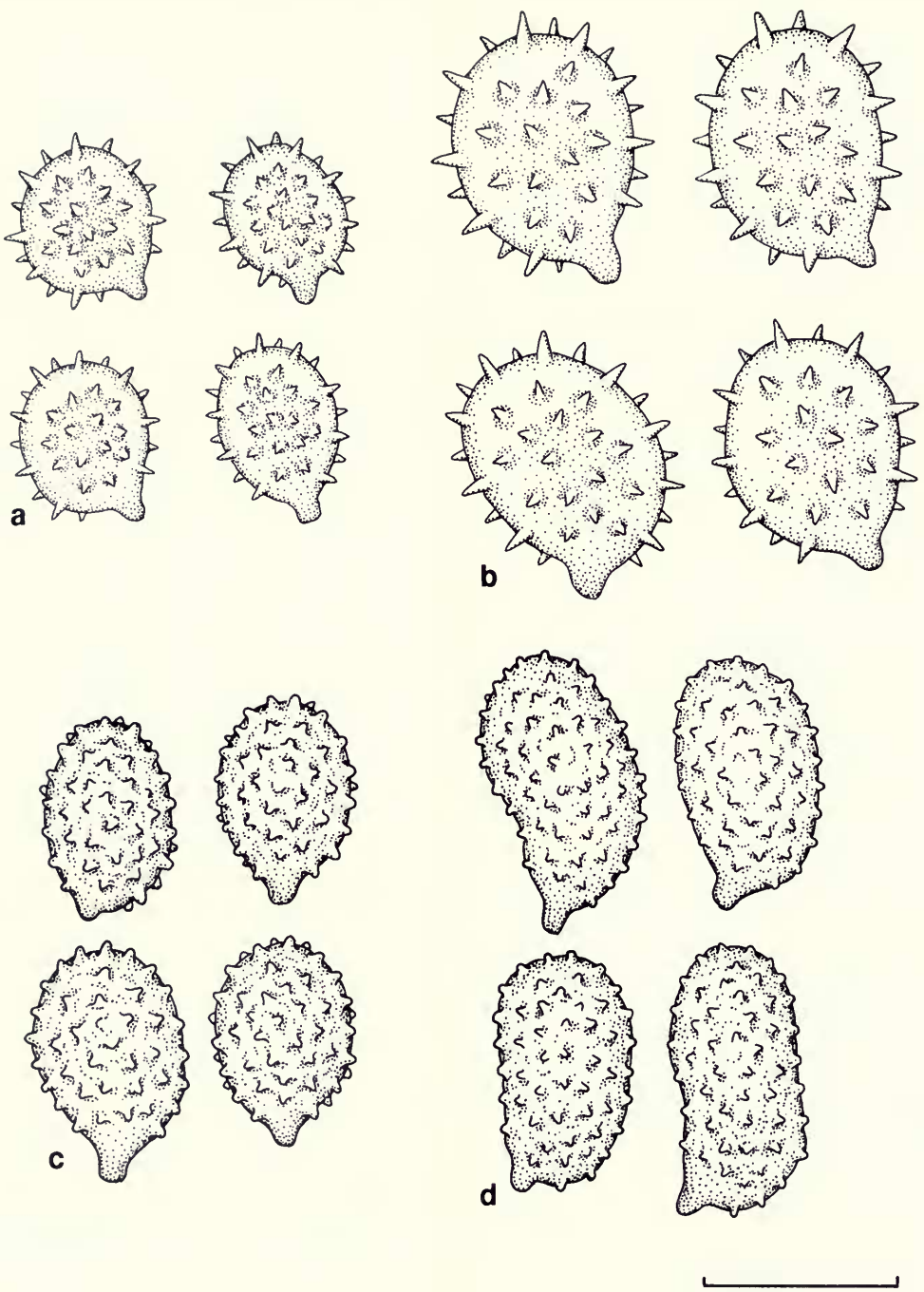


FIG. 70. Representative basidiospores from type specimens: **a,** *L. laccata* var. *pseudobicolor* (holotype); **b,** *L. pumila* (neotype); **c,** *L. purpureobadia* (holotype); **d,** *L. trullissata* f. *rugulospora* (holotype). Scale line = 10 μm.

up to 15 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (10.5–)11–15.5 × (9–)9.5–12.5(–15) μm ($\bar{x}$ = 12.5 ± 1.2 × 10.4 ± 1.1 μm), Q = (1–)1.05–1.3(–1.35) ($\bar{Q}$ = 1.18), subglobose to ellipsoid, rarely globose, hyaline, echinulate; echinulae 0.7–1.2 μm long, crowded; hilar appendix up to 2 μm long, prominent, truncate; plage present.

COMMENTARY—The type collection consists solely of lamellar fragments, so no information on pileipellis morphology could be obtained.

Although an illustration was not cited in the protologue, a watercolor housed at G reflects Fayod's concept of the taxon. The illustration matches the protologue and concept of the taxon presented here and by Mueller and Vellinga (1986).

This taxon is treated in detail in the section on North American taxa.

Laccaria purpureobadia Reid, Nova Hedwigia 11(Suppl.): 14–16. 1966. Figure 70c.

TYPE: England, Bedfordshire, Flitwick, Follywood, 11 October 1959, *Reid s.n.* (K!, holotype).

MACROMORPHOLOGY (*Teste* Reid, *ibid.*)—**Pileus** 20–55 mm broad, convex, occasionally umbonate, soon conspicuously depressed or umbilicate, minutely scurfy-scaly, hygrophanous, uniformly dark purple-brown when fresh ("Seal Brown"), fading to light purple-brown ("Sorghum Brown"); margin smooth, becoming distinctly sulcate, usually with a scaly effervescence. **Lamellae** adnexed, subdistant, up to 8 mm broad, entire, pale pinkish gray ("Pale Grayish Vinaceous") becoming pinkish purple-brown ("Livid Brown"). **Stipe** 30–60 × 3.5–8 mm, equal, slightly felty fibrillose, solid becoming hollow, purplish pink ("Light Purplish Vinaceous") at apex, dark purple-brown (between "Dark Livid Brown" and "Warm Blackish Brown") at base. **Flesh** purplish pink ("Light Purplish Vinaceous").

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–25 hyphae; terminal cells of fascicular hyphae (N = 10) 44–64(–92) × 6.5–11.5 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown, often encrusted with light yellowish brown pigments; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Pileus trama** parallel, hyphae 3–12 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 32–57.5 × 8–12.5 μm, clavate, hyaline; sterigmata 4, up to 7.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7.4–)8.3–10.6 × 6–7.8 μm ($\bar{x}$ = 9.1 ± 0.8 × 7.1 ± 0.6 μm), Q = 1.12–1.41(–1.54) ($\bar{Q}$ = 1.3 ± 0.1), broadly ellipsoid, ellipsoid, or amygdaliform, hyaline, echinulate; echinulae 0.3–0.8(–1.4) μm long; crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents uniguttulate. **Basal mycelium hyphae** mostly 4.5–15 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

COMMENTARY—Although this appears to be a discrete taxon, I cannot make a decision on the affinities of this taxon until I see fresh material. Few reports of this taxon have been published (e.g., Phillips, 1981). Singer (1986) placed it in a separate stirps, *Purpureobadia*.

Russuliopsis laccata var. **rosella** f. **pusilla** Larsen, Bot. of Iceland, vol. II, part III. 9. Fungi of Iceland. p. 525. 1932.

TYPE: Not located.

MACROMORPHOLOGY (*Teste* Larsen, *ibid.*)—**Pileus** 10–20 mm broad, depressed, thin, glabrous, pale. **Lamellae** adnate-decurrent, distant, thick, concolorous. **Stipe** short, thin, concolorous. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Teste* Larsen, *ibid.*)—**Basidiospores** 8–9 μm diam., globose, verrucose.

COMMENTARY—No authentic material of this taxon could be located at C. This name is a homonym of *R. laccata* var. *rosella* f. *pusilla* Schroeter, which is treated as a synonym of *L. laccata* var. *laccata*.

Laccaria laccata f. **retispora** Rolland, Rev. Mycol. (Toulouse) 104: 139. 1904.

TYPE: Not located.

MACROMORPHOLOGY (*Teste* Rolland, *ibid.*)—**Pileus** fresh color. **Stipe** concolorous.

MICROMORPHOLOGY (*Teste* Rolland, *ibid.*)—**Basidiospores** 10 μm diam., strongly reticulate.

COMMENTARY—Based on the original description, this taxon belongs in the Russulaceae.

Agaricus (Clitocybe) rudis Berkeley, J. Bot. (Hooker) 8: 131. 1856.

TYPE: Brazil, Rio Negro, Panure, February 1853, *Berkeley 127* (K!, holotype).

COMMENTARY—Berkeley (1856) stated that although this taxon had the same habit of *A. laccatus,* it was obviously unique. Micromorphological analysis of this collection revealed the presence of elongate, smooth basidiospores. The lack of echinulate or finely roughened basidiospores excludes it from *Laccaria.*

Agaricus (Clitocybe) laccatus var. **rufocarnea** Fries, Epicr. syst. mycol. p. 79. 1836–1838.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Fries, *ibid.*)—As in type variety, pileus becoming subochraceous when faded.

COMMENTARY—There is considerable variation in the color of faded basidiomata within *L. laccata sensu lato.* Because such variation does not justify segregation of separate taxa, this taxon is treated as a synonym of *L. laccata* var. *laccata.*

Laccaria trullisata f. **rugulospora** M. Lange, Meddel. Grønland 147: 30. 1955. Figure 70d.

TYPE: Greenland, Sondre Stromfjord, Sandflugtsdalen, 24 September 1946, *Lange 384* (C!, holotype).

MACROMORPHOLOGY (*Teste* Lange, *ibid.*)—Differs from the type variety in its smaller size.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae, no distinct fascicles of hyphae seen; terminal cells (N = 10) 33–64 × 5.5–9 μm, filamentous, subclavate or occasionally clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 5.5–11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 34–48 × 10.5–13.5(–16) μm, clavate, hyaline; sterigmata 4, up to 7.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 11.5–14.7(–15.6) × (6.4–)7.4–8.7(–9.2) μm ($\bar{x}$ = 13.3 ± 1.1 × 8.0 ± 0.6 μm), Q = 1.43–1.83 ($\bar{Q}$ = 1.67 ± 0.11), ellipsoid to oblong, hyaline, echinulate; echinulae > 0.2(–0.5) μm long, distinct, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; contents occasionally uniguttulate.

COMMENTARY—The type collection consists of small pieces of pileus. This taxon is distinguished from *L. trullissata* by having shorter, finely echinulate basidiospores.

This taxon is treated as a synonym of *L. maritima.*

Laccaria tetraspora var. **scotica** Singer, Bull. Soc. Mycol. France 83: 114, 1967. Figure 71a.

TYPE: Scotland: Lake Katrin, 1 July 1964, *Singer C4002* (BAFC!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 20–29 mm, convex, centrally depressed, umbilicate, smooth and glabrous, slightly tomentose at disc under a hand lens, hygrophanous, reddish fawn color (6 D 12, M&P), paler toward margin; margin slightly sulcate. **Lamellae** adnate, crowded, broad, dull rose color. **Stipe** usually 80 × 3.5–5.5 mm, equal or narrowing toward the base, glabrous or slightly fibrillose, stuffed, concolorous with pileus, paler or whitish toward the base. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae (N = 10) 40–55 × 5.5–10.5 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 2.5–11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 30–40 × 8–12.5 μm, clavate, hyaline; sterigmata 4, up to 12.5 μm. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 7–9.2 × 7–9.2 μm ($\bar{x}$ = 8 ± 0.6 × 7.9 ± 0.7 μm), Q = 1–1.07(–1.13) ($\bar{Q}$ = 1.01 ± 0.03), globose to subglobose, hyaline, echinulate; echinulae 1–1.8(–2.3) μm, crowded; hilar appendix 1.3–2.3 μm long, prominent, truncate; plage present;

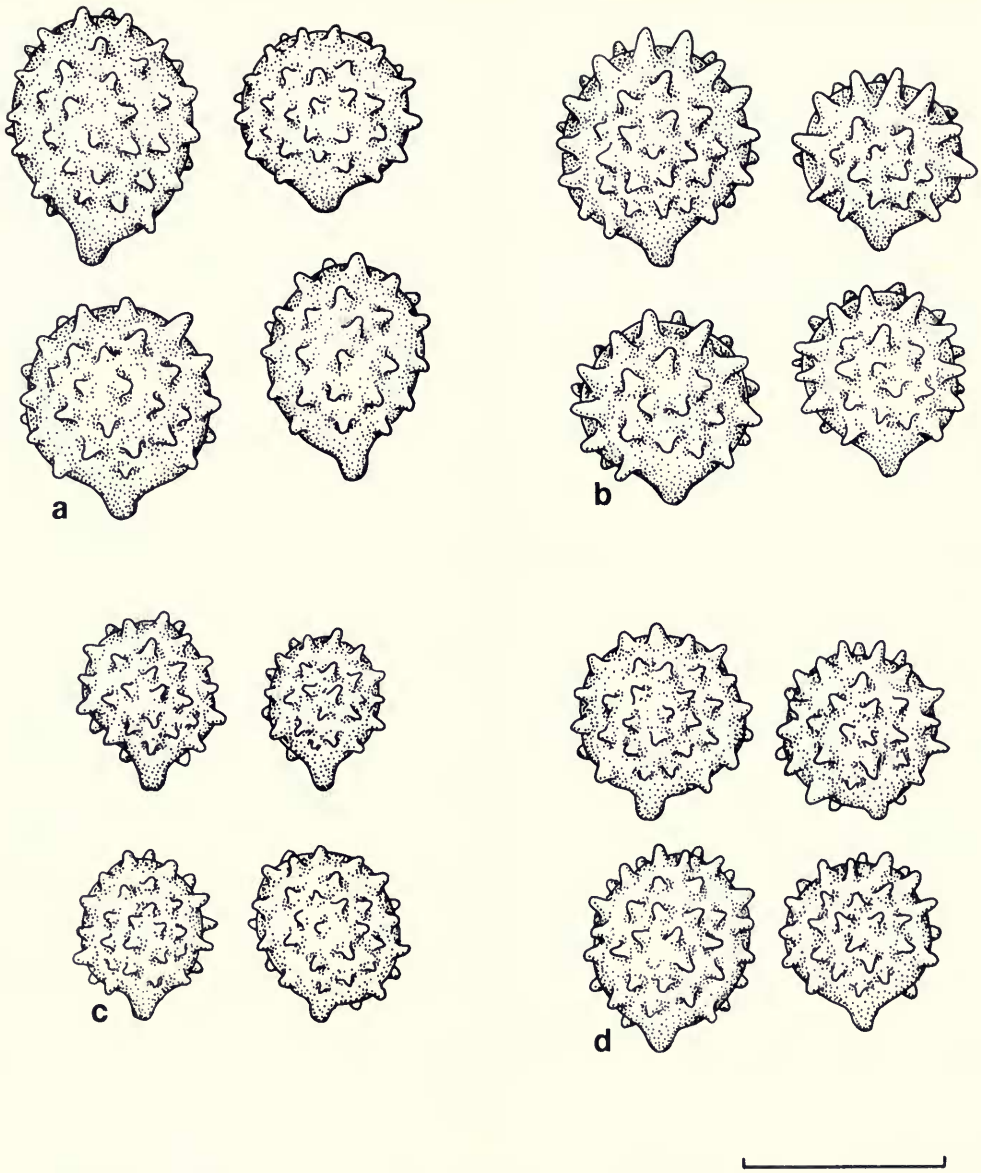


FIG. 71. Representative basidiospores from type specimens: **a,** *L. tetraspora* var. *scotica* (holotype); **b,** *C. laccata* var. *striatula* (holotype); **c,** *L. laccata* var. *subalpina* (holotype); **d,** *L. laccata* var. *tatrensis* (holotype). Scale line = 10 μm.

contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–5 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—Singer (1967) reported infrequent cheilocystidia ("cheilocystides et cystidioles éparses, 14–26 × 3 μ, filamenteuses") and the occurrence of rare 2-sterigmate basidia.

This taxon is treated as a synonym of *L. ohiensis.*

Agaricus sevocatus Britzelmayr, Hymenomyc. Südbayern, Bot. Centralbl. 54: 5, fig. 594. 1893.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Britzelmayr, *ibid.*)—**Pileus** hygrophanous, gray or brownish gray. **Lamellae** rather decurrent. **Stipe** undulating.

MICROMORPHOLOGY (*Teste* Britzelmayr, *ibid.*)—**Basidiospores** 5–7 μm diam., echinulate.

COMMENTARY—The original description stated that this taxon was similar to *A. echinosporous.* The basidiospore dimensions provided in the protologue, however, are much smaller than those found in *L. tortilis* (= *A. echinosporous*) or other known *Laccaria* species. Material that matched the protologue of this name was not encountered during this study. The decurrent lamellae and gray basidioma color suggest that this taxon may be referable to *Clitocybe,* not *Laccaria.*

Agaricus (Clitocybe) spodophorus Berkeley & Broome, J. Linn. Soc., Bot. 11: 518. 1871.

TYPE: Ceylon, September 1869, *Berkeley 1215* (K!, holotype; illustration only).

MACROMORPHOLOGY (*Teste* Berkeley & Broome, *ibid.*)—**Pileus** 13 mm broad, subhemispherical, slightly umbilicate, dull flesh color covered with black flocculent specks. **Lamellae** few, adnate with decurrent teeth; margin serrate, concolorous, with black specks. **Stipe** subclavate, concolorous, covered with fine black flocci, especially near apex, solid.

COMMENTARY—The illustration matches the protologue. Cooke (1884) included this name when he transferred taxa into *Laccaria.* Without micromorphological data, it is impossible to clarify the concept of this taxon, and its identity remains uncertain. Material that matches the protologue was not encountered during this study.

Clitocybe laccata var. **striatula** Peck, Annual Rep. New York State Bot. 48: 274. 1894. Figure 71b.

TYPE: USA, New York, Catskill Mountains, September, *C. H. Peck s.n.* (NYS!, holotype).

MACROMORPHOLOGY (*Teste* Peck, *ibid.,* 1912)—**Pileus** 12–20 mm broad, convex to plane, translucent-striate, thin, glabrous, hygrophanous, buff red, fading to grayish or pale buff. **Lamellae** adnate, distant, broad, pale flesh color. **Stipe** 15–30 × 1–2 mm, equal, fibrous, concolorous with pileus.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of tightly interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 37.5–69 × 6–12 μm, undifferentiated, yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 35–46 × 10–14 μm, clavate, hyaline; sterigmata 4, up to 10.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7–)7.8–9.7(–12) × (7–)7.8–9.7(–12) μm ($\bar{x}$ = 8.8 ± 0.9 × 8.7 ± 0.9 μm), Q = 1(–1.06) ($\bar{Q}$ = 1.0 ± 0.02), globose, occasionally subglobose, hyaline, echinulate; echinulae 1.4–2.3(–2.8) μm long, up to 1.3 μm wide at base, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–4 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.

COMMENTARY—The type collection appears mixed. Two distinct sets of basidiomata can be segregated based on basidiospore size and length of basidiospore ornamentation. Because Peck (1895, 1912) stated that the taxon had large basidiospores, the description above is based on those basidiocarps that have large basidiospores. Lahaie (1981) concurred with this segregation of the type collection.

This taxon is treated in detail in the section on North American taxa.

Laccaria laccata var. **subalpina** Singer, Pl. Syst. Evol. 126: 365. 1977. Figure 71c.

TYPE: CSSR, Slovakia, Hohe Tatra, Solisko, 4 September 1974, *Singer C5870* (F!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** ± 26 mm broad, convex, glabrous, radially striate, slightly pellucid, hygrophanous, flesh brown, fading to pale flesh color; margin sinuous. **Lamellae** adnate, crowded to distant, moderately broad, dirty pale lilac-pink to violet pink when young, soon becoming flesh-rose color. **Stipe** 40–45 × 3.5–4 mm, equal, striate, tortulous, coarsely fibrous, not woolly or hoary, flesh-brown to brown. **Basal mycelium** white.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; terminal cells of fascicular hy-

phae (N = 10) 39–57.5 × 8–13 μm, filamentous to subclavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 32–42 × 8–9.5(–11) μm, clavate, hyaline; sterigmata 4, up to 6.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 5) 30.5–35 × 3.5–4.5 μm, filamentous to subclavate, abundant, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) (6.4–) 7–7.8(–8.3) × (6–)6.4–7.4 μm ($\bar{x}$ = 7.5 ± 0.5 × 6.8 ± 0.3 μm), Q = 1–1.16(–1.22) ($\bar{Q}$ = 1.1 ± 0.06), subglobose or occasionally globose, hyaline, echinulate; echinulae (0.8–)1.4–1.8 μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** 2.5–11 μm diam.; tightly interwoven, hyaline; cells barrel-shaped.

COMMENTARY—Although the basidiospore shape and size fit the original circumscription, basidiospore ornamentation was longer than that reported by Singer (1973).

This taxon is treated as a synonym of *L. laccata* var. *pallidifolia.*

Agaricus (Clitocybe) sublaccatus Berkeley & Broome, J. Linn. Soc., Bot. 11: 519. 1871.

TYPE: Ceylon, Peradeniya, January 1869, *Berkeley 894* (K!, holotype).

COMMENTARY—Micromorphological analysis of this collection revealed the presence of ellipsoid, smooth basidiospores. Although Cooke (1884) included this name when he transferred taxa into *Laccaria,* the lack of echinulate or finely roughened basidiospores excludes it from *Laccaria.*

Laccaria laccata var. **tatrensis** Singer, Pl. Syst. Evol. 126: 367–368. 1977. Figure 71d.

TYPE: CSSR, Slovakia, Hohe Tatra, Mala Studena Dolina, 13 September 1974, *Singer C6001* (F!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 14–20 mm broad, convex, not umbilicate or umbonate, moderately depressed in age, glabrous, in age appearing subtomentose, fibrous, or subsquamulose under hand lens, translucent striate at margin, hygrophanous, reddish cinnamon to dark ochre reddish brown, fading to pallid flesh color. **Lamellae** adnate to subdecurrent, subdistant, flesh-colored rose when fresh. **Stipe** 24–35(–50) × 2–3.5(–7) mm, equal or rarely thickened at base; at first glabrous, becoming sulcate and rough, flesh-colored brown to almost reddish brown, drying paler. **Basal mycelium** white. **Basidiospores** white in mass. **Odor** lacking or slightly raphanoid.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 15–25 hyphae; terminal cells of fascicular hyphae (N = 10) 36–55 × 4–9 μm, filamentous, subclavate or subcapitate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 3–13.5 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 27.5–40.5 × 10–12.5 μm, clavate, hyaline; sterigmata 4, occasionally 2, up to 9 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 24.5–55 × 3.5–6 μm, thin, filamentous to subclavate, abundant, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) 7.4–9.2 × 7.4–9.2 μm ($\bar{x}$ = 8.4 ± 0.6 × 8.2 ± 0.6 μm), Q = 1–1.11(–1.12) ($\bar{Q}$ = 1.03 ± 0.04), globose, rarely subglobose, hyaline, echinulate; echinulae 1–1.8 μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–7 μm diam.; morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—This taxon is treated as a synonym of *L. laccata* var. *pallidifolia.*

Laccaria tetraspora Singer, Mycologia 38: 689–690. 1946. Figure 72a.

TYPE: USA, Florida, Sebring Co., Highlands Hammock State Park, 11 July 1942, *Singer F16C* (FH!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 10–20 mm broad, convex, becoming plane and depressed, usually umbilicate, glabrous or fibrillose, pellucid, hygrophanous, rose flesh-col-

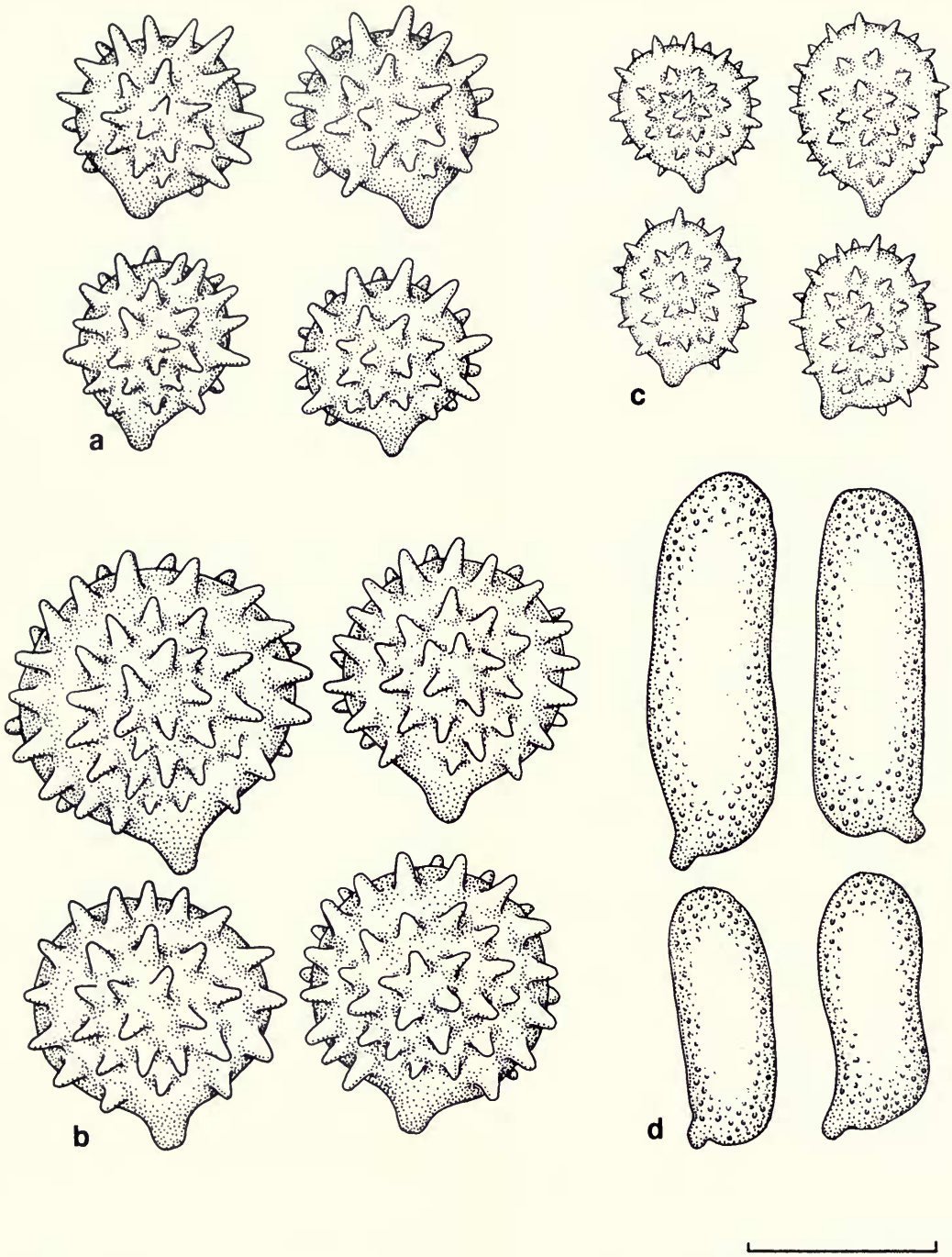


FIG. 72. Representative basidiospores from type or representative specimens: **a,** *L. tetraspora* (holotype); **b,** *A. tortilis* (representative specimen); **c,** *L. trichodermophora* (holotype); **d,** *A. trullissatus* (lectotype). Scale line = 10 μm.

ored ("incarnato-rosea," Singer) or brownish flesh-colored ("brunneolo incarnato," Singer) when moist, pale purple-pink ("pallid-purpurascente-rosello," Singer) when dry; margin striate when fresh, sulcate when dry. **Lamellae** adnate to decurrent, distant, broad, rose flesh-colored ("incarnato-roseis," Singer), pulverulent from basidiospores. **Stipe** 10–30 × 1.5–2.5 mm, equal or with expanded base, dry, subglabrous, solid, almost concolorous with pileus. **Basal mycelium** white, scant to copious.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; terminal cells of fascicular hyphae (N = 10) 26–62 × 7.5–11.5 μm, filamentous, subclavate or subcapitate, light yellowish brown in mass; walls up to 0.5 μm thick, pale yellowish brown; contents hyaline in mass. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 3–15 μm, thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 42–55 × 10–13 μm, clavate, hyaline; sterigmata 4, up to 8.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7.8–)8.7–11 × 8.3-10(–10.6) μm ($\bar{x}$ = 9.3 ± 0.7 × 9.1 ± 0.5 μm), Q = 0.94–1.2 ($\bar{Q}$ = 1.02 ± 0.1), globose to subglobose, hyaline, echinulate; echinulae (0.8–)1.4–2.3(–2.8) μm long, relatively sparse; hilar appendix 1.8–2.3 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–5 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.

COMMENTARY—Singer (1946) reported the presence of inconspicuous cheilocystidia ("cheilocystids praesentibus sed haud conspicuis"). The discrepancy between Singer's description and my observations may be due to poor rehydration of the specimen or to the absence of cheilocystidia in the preparations examined.

This taxon is treated as a synonym of *L. ohiensis*.

Russuliopsis thymiphila Velenovsky, Novitates Mycologicae. p. 77. 1939.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Velenovsky, *ibid.*)—**Pileus** 3–6 mm broad, convex, becoming plane, finely rimose, hygrophanous, cinnamon color when fresh, becoming ochraceous. **Lamella** adnate to arcuate, crowded, thick, broad, flesh color to cinnamon color. **Stipe** 3 times longer than pileus diameter, flexuous, glabrous, concolorous.

MICROMORPHOLOGY (*Teste* Velenovksy, *ibid.*)—**Basidiospores** 5–7 μm diam., globose, smooth, uniguttulate, hyaline.

COMMENTARY—Type material of this taxon was not found at either PRM or PRC. Based on the original description, it is not a *Laccaria,* but there is insufficient data for an accurate determination of the disposition of this taxon.

Agaricus tortilis Bolton, Hist. Fung. Halifax vol. 1. p. 41, tab. XLI, fig. A. 1788. Figure 72b.

TYPE: Tab. XLI, fig. A. in Bolton, Hist. Fung. Halifax vol. 1. 1788 (lectotype *fide* Mueller, 1991a). Representative specimen: Scotland, Yorkshire, Tanfield Lodge, 6 September 1969, *Orton 3642* (E!, "neotype" *fide* Mueller, 1987).

MACROMORPHOLOGY (*Teste* Bolton, *ibid.*)—**Pileus** very small to small, convex, becoming plane to uplifted, striate, dark reddish brown; margin lobed, crumpled and distorted. **Lamellae** dusky color. **Stipe** 6 mm long, dusky flesh color.

MICROMORPHOLOGY (*Mihi,* From representative specimen)—**Pileipellis** of interwoven hyphae with scattered fascicles or ± perpendicular hyphae; terminal cells of fascicular hyphae (N = 5) 32–55 × 6.5–12.5 μm, filamentous, subclavate or occasionally clavate; walls up to 0.5 μm thick, pale yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae 3–13 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 40–60 × 9–13 μm, clavate, hyaline; sterigmata 2, up to 11 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) 11.5–14.7(–17) × 11.5–14.7(–17) μm ($\bar{x}$ = 13.4 ± 1.3 × 13.4 ± 1.3 μm), Q = 1(–1.04) ($\bar{Q}$ = 1 ± 0.01), globose, hyaline, echinulate; echinulae 2.3–4 μm long, 1.3–1.8 μm wide at base, crowded; hilar appendix 1.3–2.3 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–5.5 μm diam., tightly interwoven, morphologically undifferentiated, hyaline.

COMMENTARY—At least two conflicting interpretations of this epithet have been used, based on the macromorphological information available in Bolton's (1788) protologue and illustration (Mueller, 1987). As discussed in the Commentary under the type of *L. proxima,* conflicting interpretations of epithets are not always resolved by designating illustrations as lectotypes. To stabilize the application of *L. tortilis,* the collection that was proposed as a neotype by Mueller (1987) was redesignated as a representative specimen (Mueller, 1991a).

Although no specimen of *A. tortilis* is available from the vicinity of Halifax, owing to disruption of the original habitat, the representative specimen was collected in an area similar to Bolton's original collecting sites (R. Watling, pers. comm.). Although the collection lacks morphological notes, it shows obvious resemblance to Bolton's plate and fits well within the circumscription of the common usage of the epithet.

Laccaria trichodermophora G. M. Mueller, Mycotaxon 20: 112–114. 1984. Figure 72c.

TYPE: USA, Mississippi, Harrison Co., DeSoto National Forest, Harrison Experimental Forest, Road H-6, 5 December 1980, *G. M. Mueller 1062* (TENN 42523) (TENN!, holotype).

MACROMORPHOLOGY (*Mihi*)—**Pileus** 6–40 mm broad ($\bar{x}$ = 21 mm), convex to plane, becoming uplifted, occasionally depressed, not striate, finely fibrillose when young, becoming finely scaly due to cuticular defraction, hygrophanous, brownish orange ("Auburn," "Sanford's Brown," "Burnt Sienna," or "Cinnamon-Rufous"), occasionally darker at disc ("Kaiser Brown"); margin decurved to plane, entire to eroded; context 1–2 mm thick, tapering quickly to margin, flesh-colored ("Pale Vinaceous-Pink"). **Lamellae** sinuate to adnate, close to subdistant, thin, flesh-colored ("Pale Flesh Color" to "Salmon-Buff"). **Stipe** 25–85 × 2–7 mm ($\bar{x}$ = 53 × 4 mm), equal or occasionally tapering toward base, dry, finely fibrillose, inconspicuously striate, brownish orange to reddish brown ("Hazel," "Pecan Brown," "Cacao Brown," or "Kaiser Brown"), context stuffed becoming hollow, flesh-colored ("Hydrangea-Pink" to "Pale Vinaceous-Pink"). **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with numerous large fascicles of ± perpendicular hyphae, forming a trichodermium in young specimens and at the disc; fascicles composed of more than 30 hyphae; terminal cells (N = 10) 29–69 × 12–20 μm, filamentous, clavate or occasionally capitate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline to light yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 5.5–11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 10) 31–43 × 7.5–10.5 μm, clavate, hyaline; sterigmata 4, up to 6 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (6.8–)7.4–9.2 × 6.4–8.3 μm ($\bar{x}$ = 7.9 ± 0.5 × 7.2 ± 0.6 μm), Q = 1–1.22 ($\bar{Q}$ = 1.1 ± 0.06), subglobose to broadly ellipsoidal, infrequently globose, hyaline, echinulate, echinulae 0.8–1.8 μm long; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–5.5 μm diam., hyaline, morphologically undifferentiated.

SOMATIC CULTURE MAT MORPHOLOGY—**PDA: Radius** at week 3 = 15–19 mm, week 6 = 32–38 mm; **mat** felty, moderately thick, tightly interwoven, tightly appressed to agar surface, in time forming pruinose aerial layer away from plug, not translucent, deep bright violet, fading to violet, finally to light orange-brown near plug; **margin** up to 4 mm broad, silky to subfelty, thin, entire to slightly uneven, light violet to white; **plug** concolorous with mat; **hyphae** mostly morphologically undifferentiated, occasional subcoralloid or irregularly swollen. **MMN: Radius** at week 3 = 26–44 mm, week 6 = 54–62 mm; **mat** subfelty, becoming felty, thin, with 2 or 3 narrow (2–3 mm) slightly thicker concentric zones, interwoven, tightly appressed to agar surface, slightly translucent, light violet, thicker zones somewhat darker; **margin** not well differentiated from mat, silky to subfelty, sinuate, light violet; **plug** concolorous with mat; **hyphae** mostly morphologically undifferentiated, occasionally subcoralloid. **MEA: Radius** at week 3 = 20–22 mm, week 6 = 38–47; **mat** subfelty, thin, loosely interwoven, tightly appressed to agar surface, translucent, white; **margin** 1–2 mm broad, thin, silky, becoming subfelty, entire, white; **plug** white; **hyphae** mostly morphologically undifferentiated, occasionally irregularly swollen.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

Agaricus (Clitocybe) trullissatus Ellis, Bull. Torrey Bot. Club 5: 45. 1874. Figure 72d.

TYPE: USA, New Jersey, Newfield, no date, *Ellis s.n.* (NYS!, lectotype *fide* Mueller, 1987).

MACROMORPHOLOGY (*Teste* Ellis, *ibid.*)—**Pileus** plano-convex, becoming depressed, fibrose-squamose, smoother at disk, fleshy; margin thin. **Lamellae** adnate with decurrent tooth, distant, coarse, thick, unequal, purple-violet, becoming dark brick red, white pulverulent. **Stipe** club-shaped, radicating, fibrillose, stuffed; flesh violet-purple; stipe base tomentose, covered with sand.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with widely scattered fascicles of ± perpendicular hyphae, fascicles composed of 10–25 hyphae; terminal cells of fascicular hyphae (N = 10) 33–64.5 × 8.5–14(–16) μm, subclavate, clavate or broadly clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 6.5–14.5 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 30–53 × 9–12.5 μm, clavate, hyaline; sterigmata 4, up to 8 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (N = 30) (13.8–)14.7–21.6(–36.3) × (5.5–)6–7.8(–8.3) μm ($\bar{x}$ = 18.9 ± 4.0 × 6.8 × 0.7 μm), Q = 1.99–3.31 (–6.05) ($\bar{Q}$ = 2.68 ± 0.7), subfusiform to fusiform-ellipsoidal, hyaline, finely roughened, not echinulate; hilar appendix 1.3–1.8 μm long, prominent, truncate; contents occasionally uniguttulate, rarely biguttulate. **Basal mycelium hyphae** mostly 3–15 μm diam., tightly interwoven, hyaline; cells filamentous to barrel-shaped.

COMMENTARY—Ellis (1874) did not designate a type. Two possible sources for a type exist: (1) the collection at NYS labeled COTYPE, which included a note in Ellis's handwriting giving collection data and stating that it is a new species; and (2) specimens in Ellis's exsiccata "Fungi of North America." Because the exsiccata was not distributed until 1875–1885 (Stafleu & Cowan, 1976), there is no way of knowing if the included specimens of *A. trullissatus* were in Ellis's hands at the time he designated the species. For these reasons, I have chosen to designate the NYS collection as the lectotype and consider the material in the exsiccata as authentic material.

This taxon is treated in detail in the section on North American taxa.

Laccaria tetraspora var. **valdiviensis** Singer, Bull. Soc. Mycol. France 83: 113. 1967. Figure 73a.

TYPE: Chile, Valdivia, Cordillera Pelada, El Mirador, 28 March 1963, *Singer M3191* (BAFC!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 13–21 mm broad, soon concave (13 B 9/11, M&P). **Lamellae** broad, rounded, not decurrent (10 A 6, M&P). **Stipe** 43–56 × 2.3–3.5 mm, 5–10 mm broad at widest point, more or less ventricose, near (7 H 12, M&P). **Basal mycelium** white.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 10–20 hyphae; terminal cells of fascicular hyphae (N = 10) 40–60 × 7.5–17.5 μm, subclavate to clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 4–12.5 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 34–48 × 10–13.5 μm, clavate, hyaline; sterigmata 4, up to 9 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7–)7.8–9.2(–10) × (7–)7.8–9.2(–10) μm ($\bar{x}$ = 8.4 ± 0.6 × 8.3 ± 0.6 μm), Q = 1–1.06 ($\bar{Q}$ = 1.0 ± 0.02), globose, rarely subglobose, hyaline, echinulate; echinulae 0.8–1.8 μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–4.5 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—The holotype consists of a single damaged basidioma in which many of the lamellae have been eaten by insects.

This taxon is treated as a synonym of *L. ohiensis*.

Laccaria vinaceoavellanea Hongo, Mem. Shiga. Univ. 21: 62. 1971. Figure 73b.

TYPE: Japan, Nango-Imodani, Otsu, 11 July 1970, *Hongo 4160* (Herbarium Hongo!, holotype).

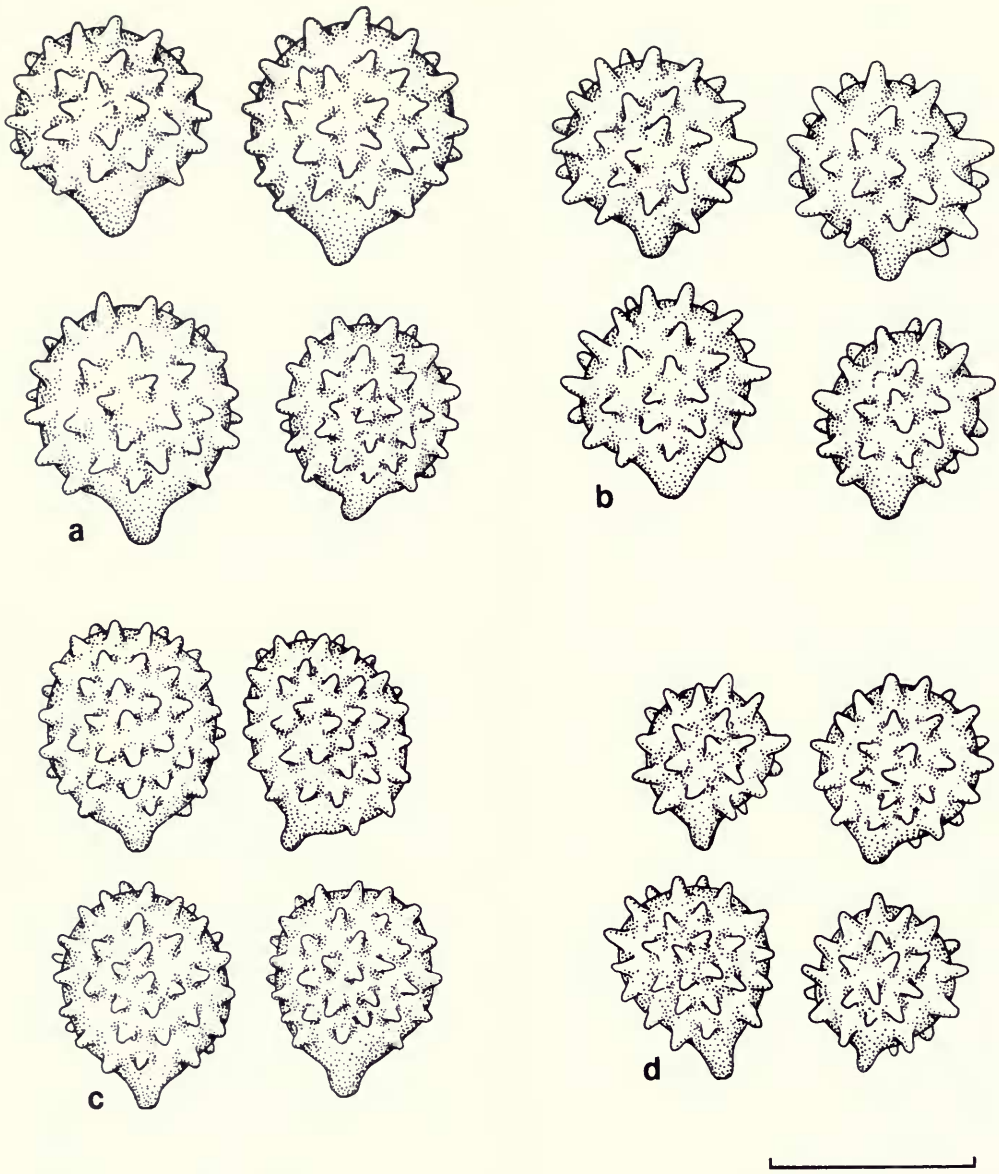


FIG. 73. Representative basidiospores from type specimens: **a,** *L. tetraspora* var. *valdiviensis* (holotype); **b,** *L. vinaceoavellanea* (holotype); **c,** *L. vinaceobrunnea* (holotype); **d,** *L. violaceoniger* (holotype). Scale line = 10 μm.

MACROMORPHOLOGY (*Teste* Hongo, *ibid.*)—**Pileus** 40–60 mm broad, convex, becoming expanded, occasionally umbilicate or depressed, not viscid, radially striate, subsulcate, furfuraceous, especially at disc, brownish vinaceous ("Russet-Vinaceous," "Vinaceous-Buff," etc.); flesh thin, firm, concolorous, with slight farinaceous odor. **Lamellae** adnate to subdecurrent, distant, thick, 4–6 mm broad, subconcolorous. **Stipe** 50–80 × 6–8 mm, equal, firm, fibrous, striate, concolorous with pileus, solid or hollow. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–10 hyphae; terminal cells of fascicular hyphae (N = 10) 34.5–48 × 6–10.5 μm, filamentous, subclavate or clavate, light yellowish brown in mass; walls up

to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 28.5–39 × 8.5–13.5 μm, clavate, hyaline, not rehydrating well; sterigmata 4, up to 8 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (6.4–)7.4–9.2(–9.7) × (6.4–)7.4–9.2(–9.7) μm ($\bar{x}$ = 8.2 ± 0.7 × 8.06 ± 0.7 μm), Q = 1–1.06(–1.12) ($\bar{Q}$ = 1.02 ± 0.03), globose to subglobose, hyaline, echinulate; echinulae 1.4–2.8(–3.2) μm long, not crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3.5–7 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—This taxon can be separated from *L. laccata* by its darker, dull color (Hongo, 1971).

Laccaria vinaceobrunnea G. M. Mueller, Mycotaxon 20: 114–115. 1984. Figure 73c.

TYPE: USA, Louisiana, Tammany Parish, Fontainebleu State Park, under *Quercus virginiana,* 9 December 1980, *G. M. Mueller 1120* (TENN 42525) (TENN!, holotype).

MACROMORPHOLOGY (*Mihi*)—**Pileus** 7–26 mm broad ($\bar{x}$ = 15 mm), convex, depressed, occasionally striate when wet, finely fibrillose, occasionally becoming finely scaly, hygrophanous, when young and fresh brownish vinaceous ("Dark Vinaceous-Brown" to "Hay's Brown") becoming reddish brown ("Walnut Brown" to "Cameo Brown"), fading lighter (near "Cinnamon-Rufous" to "Light Ochraceous-Buff"); margin decurved to plane, entire to eroded; context 1–2 mm thick, tapering quickly to margin, light brownish vinaceous ("Light Brownish Vinaceous" to "Vinaceous-Fawn"). **Lamellae** adnate to arcuate, subdistant, thick, broad, violaceous to vinaceous ("Purplish Lilac" to "Purplish Vinaceous"). **Stipe** 7–48 × 2–6 ($\bar{x}$ = 25 × 3.5 mm), equal, occasionally bulbous, dry, fibrillose, some fibrils recurved, not striate, ± concolorous with pileus, when young and at apex ("Brownish Vinaceous" to "Deep Brownish Vinaceous"), some fading to orange-brown (near "Hazel"); ground color buff (near "Light Ochraceous Buff"); fibrils darker ("Hazel" to "Vinaceous-Brown"). **Basal mycelium** violet. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with numerous ± perpendicular hyphae, nearly forming a palisadoderm; terminal cells (N = 10) 42–50.5 × (4.5–)8.5–10 μm, filamentous to clavate, hyaline to light vinaceous; walls up to 0.5 μm thick; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline to light olive brown in mass. **Lamellar trama** parallel; hyphae thin-walled, hyaline; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 10) 42–50.5 × (4.5–)8.5–10 μm, clavate, hyaline, sterigmata 4, up to 8.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) 31.5–64.5 × 5.5–11 μm, filamentous to clavate, abundant, hyaline. **Basidiospores** (excluding ornamentation) (N = 30) (7.4–)8.3–10 × (6.4–)7–8.7(–9.2) μm ($\bar{x}$ = 9 ± 0.7 × 7.8 ± 0.6 μm), Q = 1.05–1.24 ($\bar{Q}$ = 1.15 ± 0.05), subglobose to ellipsoid, hyaline, echinulate; echinulae 0.8–1.8 μm long, crowded; hilar appendix 1.3–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–5.5 μm diam., tightly interwoven, hyaline.

COMMENTARY—This taxon is treated in detail in the section on North American taxa.

Agaricus (Clitocybe) laccatus var. **[obscure] violacea** Fries, Epicr. syst. mycol. p. 79. 1836–1838.

TYPE: Lacking.

MACROMORPHOLOGY (*Teste* Fries, *ibid.*)—**Pileus** drying grayish.

COMMENTARY—Much variation exists in the color of dried basidiomata of *Laccaria* and this character should not be used to delimit taxa. This taxon, therefore, is treated as a synonym of *L. laccata* var. *laccata.*

Laccaria violaceoniger Stevenson, Kew Bull. 19: 4. 1964. Figure 73d.

TYPE: New Zealand, Nelson, Dun Mt. tract, 25 April 1949, *Stevenson 506* (K!, holotype).

MACROMORPHOLOGY (*Teste* Stevenson, *ibid.*)—**Pileus** 15–35 mm broad, convex, becoming plane, appearing velvety owing to small floccose scales,

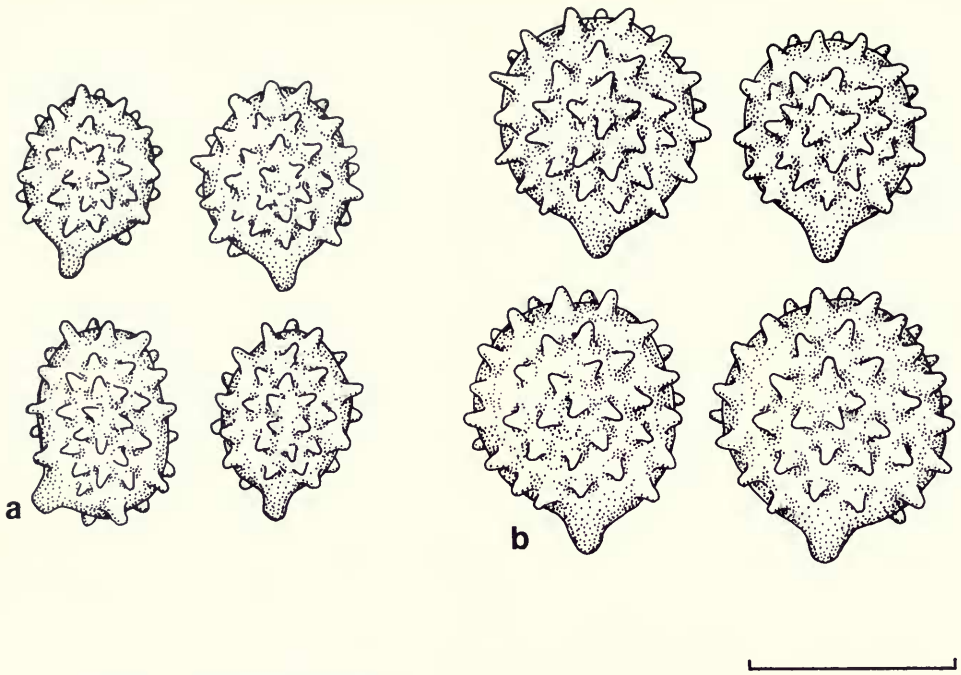


FIG. 74. Representative basidiospores from type or representative specimens: **a,** *L. laccata* var. *vulcanica* (holotype); **b,** *L. tetraspora* var. *xena* (representative specimen). Scale line = 10 μm.

fuscous black; margin inrolled. **Lamellae** adnexed to decurrent, thick, purple to grayish lavender, often with white mealiness. **Stipe** 25–50 × 3–10 mm, swollen at base, floccose striate to subscaly; apex purple; base vinaceous brown.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with numerous scattered large fascicles of ± perpendicular hyphae; fascicles composed of 10–30 hyphae; terminal cells of fascicular hyphae (N = 10) 24–67 × 8–11, filamentous, subclavate, clavate or occasionally apiculate, dark yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents dark yellowish brown. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–10 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 31–47 × 8.5–11.5 μm, clavate, hyaline; sterigmata 4, up to 6 μm long. **Pleurocystidia** lacking. **Cheilocystidia** (N = 10) (21–)29–39 × 2.5–6.5 μm, thin, filamentous, subclavate or strangulose, scattered, hyaline; lamellar edge nearly sterile. **Basidiospores** (excluding ornamentation) (N = 30) (6.4–)7–7.8 × (6.4–)7–7.8 μm ($\bar{x}$ = 7.4 ± 0.4 × 7.3 ± 0.4 μm), Q = 1–1.07 (–1.13) ($\bar{Q}$ = 1.02 ± 0.03), globose, occasionally subglobose, hyaline, echinulate; echinulae 0.8–1.8 (–2.3) μm long, crowded; hilar appendix 1.3–2.3 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 3–7 μm diam., morphologically undifferentiated, tightly interwoven, hyaline; walls up to 0.5 μm thick.

COMMENTARY—The affinities of this taxon with other species of *Laccaria* are unknown. The coloration of the basidioma given in the protologue is unique in the genus.

Laccaria laccata var. **vulcanica** Singer *ex* Veselsky & Singer *in* Singer, Pl. Syst. Evol. 126: 362–363. 1977. Figure 74a.

TYPE: CSSR, Moravia, Ostrava, Halde Lucina, 30 July 1968, *Veselsky s.n.* (F!, holotype).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 17–45 mm broad, convex, applanate to centrally depressed or with flat umbilicus, often umbonate in age, finely fibrous-scaly or granular scaly, becoming scaly due to cuticular diffraction, slightly hygrophanous, moderately deep flesh-brown rust

color (near 6 I 10, M&P); margin bright orange-brown to flesh color or subconcolorous. **Lamellae** adnate to subdecurrent, crowded, becoming subdistant, up to 8 mm broad, ventricose, whitish flesh color at first, becoming pale purple or pale lilac, covered with white spores. **Stipe** 25–90 × 2.5–14 mm, equal or tapering toward apex, almost glabrous when young, longitudinally striate when mature, ± concolorous with pileus. **Basal mycelium** white.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered, large fascicles of ± perpendicular hyphae; fascicles composed of 15–30 hyphae; terminal cells of fascicular hyphae (N = 10) 38–69 × 6.5–14.5 μm, filamentous, subclavate or clavate, light yellowish brown in mass; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel to subparallel; hyphae 2.5–9 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 33–44 × 8–11 μm, clavate, hyaline; sterigmata 4, up to 7 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7.4–)8.3–9.7(–11) × (6–)6.4–7.8(–8.7) μm ($\bar{x}$ = 9 ± 0.7 × 7.1 ± 0.5 μm), Q = (1.16–)1.2–1.33(–1.45) ($\bar{Q}$ = 1.27 ± 0.06), broadly ellipsoid to ellipsoid, hyaline, echinulate; echinulae 0.5–1.4(–1.8) μm long, crowded; hilar appendix 1.3–1.8 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 4–22 μm diam., tightly interwoven, hyaline to light yellowish brown in mass; cells occasionally morphologically undifferentiated, barrel-shaped.

COMMENTARY—Singer (1977) reported sparse cheilocystidia ("cystidiis vesiculosis inconstanter et sparse praesentibus"). The discrepancy between Singer's description and my observation may be due to poor rehydration or to the absence of cheilocystidia in the examined preparations.

This taxon is treated as a synonym of *L. laccata* var. *laccata*.

Laccaria tetraspora var. **xena** Singer, Bull. Soc. Mycol. France 83: 116. 1967. Figure 74b.

TYPE: Argentina, Neuquén, Bahía Lopez, 22 November 1964, *Singer M4063* (BAFC!, lectotype *nov.*).

MACROMORPHOLOGY (*Teste* Singer, *ibid.*)—**Pileus** 8–25 mm broad, hemispherical-convex at first, becoming applanate or irregularly depressed, ± glabrous, slightly pellucid-striate, hygrophanous, dull flesh-colored rose to dull rose. **Lamellae** adnate, distant, broad, dull rose-colored. **Stipe** usually 60 × 5 mm, equal, compressed or irregular, subglabrous or slightly fibrillose, reddish brown to rose brown. **Basal mycelium** white. **Basidiospores** white in mass.

MICROMORPHOLOGY (*Mihi*)—**Pileipellis** of interwoven hyphae with scattered fascicles of ± perpendicular hyphae; fascicles composed of 5–15 hyphae; terminal cells of fascicular hyphae (N = 10) 39–64 × 5–9.5 μm, filamentous, subclavate or rarely clavate; walls up to 0.5 μm thick, light yellowish brown; contents hyaline. **Pileus trama** tightly interwoven, morphologically undifferentiated, hyaline, light yellowish brown toward pileipellis. **Lamellar trama** parallel; hyphae mostly 3–11 μm diam., thin-walled, hyaline to light yellowish brown; cells barrel-shaped. **Subhymenium** morphologically undifferentiated. **Basidia** (N = 15) 39–53 × 10–13 μm, clavate, hyaline; sterigmata 4, up to 9.5 μm long. **Pleurocystidia** lacking. **Cheilocystidia** not observed. **Basidiospores** (excluding ornamentation) (N = 30) (7–)7.8–9.7 × (7–)7.8–9.7 μm ($\bar{x}$ = 8.6 ± 0.7 × 8.6 ± 0.7 μm), Q = 1(–1.05) ($\bar{Q}$ = 1 ± 0.01), globose, rarely subglobose, hyaline, echinulate; echinulae (0.8–)1.4–2.3 μm long, crowded; hilar appendix 1.4–2 μm long, prominent, truncate; plage present; contents occasionally uniguttulate. **Basal mycelium hyphae** mostly 2–5 μm diam., morphologically undifferentiated, tightly interwoven, hyaline.

COMMENTARY—In the protologue, Singer (1967) cited four collections that he had studied but failed to designate a type specimen. Of the three collections sent from BAFC and all cited by Singer, Singer M4063 had the largest number of basidiomata and was in the best condition. Collection Singer M4063 was designated the neotype for these reasons.

Singer (1967) reported the basidiospore ornamentation length as '1,0–1,5 μ," which is smaller than that presented above. The major delimiting character between var. *xena* and var. *tetraspora* is that the former has relatively shorter basidiospore ornamentation. The discrepancy between Singer's data and mine, therefore, becomes significant. He also reported the occasional presence of bisterigmate basidia, which I did not see in the collection that I examined.

This taxon is treated as a synonym of *L. ohiensis*.

Additions to Type Studies

Laccaria laccata var. **crispa** A. Thesleff, Bidrag till Kännedom af Finlands natur och folk 79: 46. 1920.

TYPE: Finland.

COMMENTARY—I have not examined the type specimen or seen the description for this taxon. The epithet is listed in *Index of Fungi,* vol. 5, part 18, 1989.

Laccaria affinis f. **macrocystidiata** Migliozzi and Lavorato, Mic. Ital. 2: 6. 1988.

TYPE: Italy, Castelfusano-Roma, *no. 148/87* (herbarium V. Migliozzi, holotype).

COMMENTARY—This taxon differs from the type variety by having large cheilocystidia (45–80 [–110] × 9–14[–16] μm). Although it is not listed in the synonymy section, I treat this taxon as a synonym of *L. laccata* var. *pallidifolia.*

Laccaria affinis var. **ochrosquamulosa** Ballero and Contu, Candollea 42: 608. 1987.

TYPE: Sardinia, *Contu 861109/01* (CAG, holotype).

COMMENTARY—This taxon differs from the type variety by being more robust, more squamulose, and pallid ochraceous. The basidiospores are reported as being globose and 9–11.5 μm in diam. Although it is not listed in the synonymy section, I treat this taxon as a synonym of *L. laccata* var. *pallidifolia.*

Laccaria olivaceogrisea Vellinga, Sydowia 39: 224. 1986.

TYPE: India, Punjab, Kulu-valley, Manali, 24 August 1964, *Bas 4233* (L, holotype).

COMMENTARY—I have not examined the type specimen. This taxon appears to be a discrete species that is phenetically similar to *L. violaceonigra.*

Laccaria laccata var. **pruinosipes** Vellinga, Sydowia 39: 227. 1986.

TYPE: India, Uttar Pradesh, Mussooree, Oak-Villa, 16 September 1964, *Bas 4403* (L, holotype).

COMMENTARY—I have not examined the type specimen. It primarily differs from *L. laccata* var. *pallidifolia* by having short hairs that cover the stipe.

Laccaria affinis var. **sardoa** Bon and Contu, Docs. Mycol. 15: 53. 1985.

TYPE: Sardinia, *no. 84395* (herbarium M. Bon, holotype).

COMMENTARY—This taxon differs from the type variety in color (rosy) and habitat (xerophytic area under *Quercus*). Basidiospores are reported as globose with echinulae 1–1.5 μm long. Although it is not listed in the synonymy section, I treat this taxon as a synonym of *L. laccata* var. *pallidifolia.*

Laccaria singeri [sic singerii] Locquin and Sarwal in Sarwal and Locquin, Comptes rendus du 108° Congrès national des Sociétés savantes, Grenoble 1983 Section des Sciences 1: Sciences de la Terre 2: 195. 1983.

TYPE: India, Sikkim.

COMMENTARY—I have not examined the type specimen or seen the description for this taxon. The epithet is listed in *Index of Fungi,* vol. 5, part 15, 1988.

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Appendix A. Specimens Examined[1]

Laccaria amethysteo-occidentalis

CANADA

British Columbia: Victoria, Beaconhill Park, 17.XI.1941, *10686* (DAOM); same locality, 25.XI.1941, *F10688* (DAOM); Victoria Island, Saanich, Braefoot, 1.XII.1941, *F10687* (DAOM); Victoria, X.1956, *54064* (DAOM); Victoria, Thetis Park Nature Sanctuary, 7.X.1959, *67060* (DAOM); Rubble Creek, off Squamish Highway, 8.X.1966, *coll. Flegel* (NY); Alice Lake Provincial Park campground, 3.X.1981, *42526* (TENN, **Holotype**); Alice Lake Provincial Park campground, 7.X.1981, *42566* (TENN).

UNITED STATES

California: Butte Co., Paradise, 26.XI.1968, *Ripley 1626* (SFSU). Del Norte Co., Hwy. 199 at Oregon border, 29.X.1971, *Thiers 28471* (SFSU). Marin Co., Muir Woods National Monument, 29.XII.1966, *Madden 835* (SFSU); Lucas Valley, *Thiers 27112* (SFSU). Mendocino Co., near Mendocino, Jackson State Forest, 23.XI.1962, *Thiers 9497* (NY); "Aleuria Glen," 24.XI.1967, *Jordon 951* (SFSU); Jackson State Forest, 11.XII.1971, *Bigelow 17034* (MASS); same locality, 2.XII.1972, *Thiers 30872* (SFSU); same locality, 2.XII.1972, *coll. Nivison* (SFSU); same locality, *Thiers 27247* (SFSU); 23.I.1979, *Sundberg 4132* (SIU). Monterey Co., Pacific Grove, 25.I.1974, *Thiers 32180* (SFSU); Monterey, 10.III.1979, *Thiers 39586* (SFSU). Santa Barbara Co., Keniven Branch, San Marcos Pass, 13.I.1979, *250738* (LAM). San Mateo Co., San Francisco Watershed, 30.XII.1968, *Keller 292* (SFSU); same locality, 30.XII.1969, *Thiers 24662* (SFSU). Sonoma Co., Salt Point State Park, 25.XI.1972, *Thiers 30741* (SFSU). Trinity Co., Highway 299, Gray Falls campground, 18.XI.1972, *Thiers 30639* (SFSU). Tuolomne Co., Don Pedro Lake, 15.XII.1974, *Thiers 33227* (SFSU); Moccasin Point Recreation Area, Don Pedro Lake, 8.III.1979, *Thiers 39558* (SFSU); Berkeley Hills, 9.I.1914, *coll. Yates* (NY); San Francisco, Sutro Forest, 3.III.1913 (NY); 20.XII.1956, *Smith 56901* (MICH); Patrick's Point State Park, 13.XI.1957, *White 341* (MICH); Santa Barbara, Mission Canon, I–III.1913, *coll. Oleson* (NY); Santa Barbara, San Marco Pass, I–III.1913, *coll. Oleson* (NY).

Oregon: Benton Co., Corvallis, Avery Park, 3.XI.1981, *42585, 42587* (TENN); Mary's Peak, 5.XI.1981, *42586, 42589–42594* (TENN); W. L. Finley National Wildlife Refuge, 5.XI.1981, *42595* (TENN); Corvallis, 1915, *Gilbert 7194*. Lane Co., Honeyman Memorial State Park, 4.XI.1981, *42588* (TENN); Williamette National Forest, Route 242, near Limberlast campground, 6.XI.1981, *42596* (TENN). Linn Co., Cascadia State Park, 7.XI.1981, *42597* (TENN); Williamette National Forest, near Fernview campground, 7.XI.1981, *42598* (TENN). Lincoln Co., South Beach State Park, 12.XI.1981, *42600, 42601* (TENN); 1.XI.1970, *Smith 79354* (MICH). Tillamook Co., Cape Lookout State Park, 10.XI.1981, *42599* (TENN); Meriwether Dunes, near Cape Lookout, 13.XI.1981, *42602* (TENN); Mt. Hood, 25.IX.1922, *coll. Kauffman* (MICH); Takilma, 30.XI.1925, *coll. Kauffman* (MICH).

Washington: Clallam Co., Chimacum State Park, 17.X.1981, *42567* (TENN); Teal Lake Road, near port Ludlow, 17.X.1981, *42568, 42569* (TENN). Lewis Co., Cispus River, 19.X.1954, *Bigelow 2313* (MASS); Cyapus Pond, 19.X.1954, *Smith 19266* (MICH). King Co., Watermain Woods, 24.X.1981, *42565* (TENN); Seattle, X–XI.1911, *Murrill 717* (NY). Mason Co., north of Mason Lake, near Sheldon, 27.X.1981, *42563, 42564, 42570–42584* (TENN). Pierce Co., Ashford, 22.X.1954, *Bigelow 2371* (MASS); Tacoma Praires, 26.X.1911, *Murrill 717* (NY); 14.X.1915, *Kauffman s.n.* (MICH); Bremerton, XI.1930, *coll. Flett*; Longmire, 11.X.1954, *Smith 48860* (MICH); Randle, Cispus Env. Center, 22.X.1977, *Thiers 38337* (SFSU); Mt. Ranier Nat'l. Park, Tahoma Creek Rd., 15.X.1984, *E. Farwell 5015* (F).

Laccaria amethystina

CANADA

New Brunswick: Pointe a Auguste, Kouchibouguac National Park, 5.VII.1978, *169587* (DAOM); Kouchibouguac National Park, Cape St. Louis, 14.VII.1978, *169583, 169585* (DAOM).

Nova Scotia: Kings Co., Aylesford Lake, 9.VIII.1936, *110936* (DAOM); same locality, 1.IX.1972, *Harrison 11880*; Vesuvius, 7.VII.1972, *Harrison 11544* (MICH); Kentville, 25.VIII.1952, *111858* (DAOM); Paradise, 29.VIII.1953, *39102* (DAOM).

Ontario: Magnetawan, 6.IX.1921, *coll. Kelly* (MICH); Petawawa Forestry Experiment Station,

[1] Extralimital material usually is not listed except for type specimens.

24.VII.1938, *8681* (DAOM); Ramsayville, 10.VIII.1962, *89296* (DAOM); Ottawa, Cromwell Drive, 18.VII.1967, *coll. Groves & Dyer* (SFSU); St. Lawrence Island National Park, Thwartway Island, 26.VII.1976, *154695* (DAOM); same locality, 19.VIII.1976, *154694* (DAOM); same locality, 20.VIII.1976, *154693* (DAOM).

Quebec: Gatineau Park, Black Lake, 4.X.1981, *84906* (DAOM).

ENGLAND

Devon: Dartmoor, Two Bridges, Whistmans Wood, 6.IX.1971, *D. N. Pegler s.n.* (as *L. amethystea*) (K, **Neotype**).

Surrey: 16.IX.1951, *27779* (DAOM).

UNITED STATES

Colorado: Aphir, 26.VII.1956, *Smith 52886* (MICH).

Florida: Alachua Co., near Newman's Lake, 31.VII.1947, *Singer F3427* (FH). Highland Co., Highland Hammock State Park, 20.VIII.1942, *Singer F324* (FH); Planera Hammock, 24.V.1938, *18205* (FLAS).

Illinois: Jackson Co., Giant City State Park, Devils Stand Table area, 12.V.1977, *Mueller 30–32* (SIU); same locality, 8.VI.1981, *42956* (TENN); Giant City State Park campground, 15.X.1977, *Mueller 325* (SIU); *Sundberg 2663, 2665* (SIU); *Wujek 81* (SIU). Perry Co., Pyramid State Park, near Heron Pond, 16.X.1977, *Mueller 347, 365, 366* (SIU); same locality, 23.X.1977, *Mueller 377, 381* (SIU). Pope Co., Bell Smith Springs Recreation Area, 1.X.1977, *Mueller 255, 264* (SIU); same locality, 9.VI.1981, *42544* (TENN). Union Co., *West 400, 933, 973* (SIU). Williamson Co., near Devil's Kitchen Lake, 24.IX.1977, *Mueller 231, 232* (SIU); Chicago, VI.1913, *Harper 3463* (F).

Iowa: Washington Co., near English River, 26.VII.1953, *Welden C5531* (NO).

Louisiana: St. Tammany Parish, near Slidell on Military Road, 21.XI.1960, *Welden 5532* (NO).

Maine: Penobscot Co., near Norcross, 29.VIII.1962, *Bigelow 11366* (MASS). Waldo Co., Northport, Bayside Park, 9.VI.1975, *Kimball 6420* (MAINE).

Maryland: Laurel, Bells Experimental Forest, 13.IX.1969, *Miller 8069* (VPI).

Massachusetts: Stow, 24.VIII.1908, *coll. Morris & Davis* (NYS) Canton, 24.VIII.1925, *Linder 1185* (FH); Harvard, 22–24.VI.1945, *coll. Dadmum & Singer* (FH); Conway State Forest, 11.VII.1967, *Bigelow 15068* (MASS); Conway, South River area, 18.VII.1967, *Bigelow 15107* (MASS); Waban, 21.VI.1945, *coll. Southwick* (FH, **Holotype** of *L. calospora*).

Michigan: Chippewa Co., west of Detour, 23.VII.1949, *Imshaug 3916* (MICH). Livington Co., E. S. George Reserve, 12.VII.1968, *Zehner 197* (MICH). Marquette Co., Huron Mt. Club, Salmon Trout River, 2.VII.1968, *Gilliam 102* (MICH); Harlow Creek, 30.VII.1968, *Gilliam 304* (MICH); Marquette, Presque Isle City Park, 15.IX.1984, *G. M. Mueller 1919* (WTU, F). Washington Co., Winnaevana Lake, 11.VII.1970, *Smith 78363* (MICH); Mud Lake Bog, 24.IX.1978, *Smith 89333* (MICH). Washtenaw Co., Waterloo Recreation Area, 2.VII.1968, *Hoseney 826* (MICH); Burt Lake, Colonial Point, 6.IX.1969, *Bigelow 15862* (MASS).

Minnesota: Rice Co., Wheeling Township, Nerstrand State Park area, 14.VII.1965, *Weaver 1185* (MICH).

Mississippi: Pearl River Co., Pearl River, 6.VI.1976, *Bigelow 17693* (MASS).

New Hampshire: Carroll Co., Redstone, 5.IX.1963, *Bigelow 12479* (MASS); Chocorua, VIII.1918, *coll. Farlow* (FH).

New York: Albany Co., Menands, 2.VIII.1906, *coll. Peck* (NYS). Bronx Co., The New York Botanical Garden, 12.VI.1980, *coll. Rogerson* (NY). Cortland Co., south of Georgetown, near Stump Pond, 2.IX.1955, *Smith 22061* (NYS). Washington Co., Lake George Region, Mt. Hope Woods, 5.IX.1917, *4440* (CUP); Cayuga Lake Basin, North of Varna, 19.VII.1917, *24217* (CUP).

North Carolina: Chapel Hill, University of North Carolina, 19.V.1922, *Grant 5119* (NCU); same locality, 6.V.1922, *Grant 5178* (NCU).

Pennsylvania: Mt. Gretna, 3.IX.1924, *coll. Kauffman* (MICH).

Rhode Island: Beach Pond Park, 20.VII.1967, *Bigelow 15118* (MASS).

Virginia: Richmond, 10.IX.1934, *coll. Linder & Smart* (FH).

Laccaria bicolor

CANADA

British Columbia: Alice Lake Provincial Park campground, 3.X.1981, *42604, 42622–42624, 42627–42629* (TENN); same locality, 4.X.1981, *42612, 42613, 42618* (TENN); same locality, 5.X.1981, *42630* (TENN).

New Brunswick: Muchibouquac National Park, Temporary Pond, 21.IX.1978, *169575* (DAOM).

Ontario: Nipissing Dist., Algonquin Park, 11.VI.1974, *152411* (DAOM); Algonquin Provincial Park, 18.IX.1984, *G. M. Mueller 1931, 1934* (F, WTU).

UNITED STATES

Alaska: Girdwood, Alyeska Ski Area, 27.VIII.1964, *WK 1399* (TENN 42620); Girdwood Alyeska Ski Area, Winter Creek Trail, 18.IX.1969, *WK 4277* (TENN 42658); same locality, 27.VIII.1980, *WK 6396* (TENN 42659); Juneau, Mendenhall Glacier campground, 28.VII.1966, *WK 1408* (TENN 42625); Kodiak Island, 14.IX.1966, *WK 1411* (TENN 42626); Near Palmer, Finger Lake campground, 7.VIII.1967, *WK 1415* (TENN 42657); Turnagain Pass, Highway, 20.IX.1965, *WK 1405* (TENN 42609); same locality, 4.VIII.1966, *WK 1409* (TENN 42621).

California: Mendocino Co., 18.XI.1984, *G. M. Mueller 2066* (F, WTU); 2.XII.1984, *G. M. Mueller 2118* (F, WTU).

Idaho: Bonner Co., Kaniksu National Forest, West Side Priest Lake Road, 25.IX.1981, *42617* (TENN); Kaniksu National Park, Binarch Road, 26.IX.1981, *42607, 42608, 42615, 42616* (TENN); same locality, 27.IX.1981, *42619* (TENN). Boundary Co., Upper Priest River, 16.X.1972, *Smith 82905* (MICH).

Michigan: Cheboygan Co., 6.IX.1984, *G. M. Mueller 1856* (F, WTU); 10.IX.1984, *G. M. Mueller 1881* (F, WTU); Marquette Co., 13.IX.1984, *G. M. Mueller 1892* (F, WTU).

Oregon: Benton Co., Avery Park, 27.XI.1976, *38565* (OSC). Lane Co., Honeyman Memorial State Park, 4.XI.1981, *42656* (TENN); Williamette National Forest, near Limberlast campground, 6.XI.1981, *42660, 42661* (TENN). Linn Co., Cascadia State Park, 7.XI.1981, *42662* (TENN). Lincoln Co., South Beach State Park, 8.XI.1981, *42663–42666* (TENN). Maltnomah Co., Timberline Lodge Road, 9.X.1978, *Hunt 018* (OSC). Tillamook Co., Cape Lookout State Park, 10.XI.1981, *42667, 42668* (TENN); Meriwether Dunes, 13.XI.1981, *42603, 42669, 42670* (TENN); Little Nestucca Park, 13.XI.1981, *42614, 42671* (TENN). Union Co., Starkey Expt. Forest and Range, 15.X.1976, *Trappe 4755* (OSC); same locality, 16.X.1976, *Trappe 4779* (OSC).

Washington: Clallam Co., near Port Ludlow, Teal Lake Road, 17.X.1981, *42637, 42638* (TENN); Grays Harbor Co., Ocean City State Park, 20.X.1981, *42640, 42641* (TENN), same locality, 10.X.1984, *G. M. Mueller 2038* (F, WTU). King Co., Snoqualmie National Forest, Asahel Curtis Nature Trail, 13.X.1981, *42633* (TENN); Snoqualmie National Forest, Annette Lake Trail, 13.X.1981, *42606* (TENN); near Redmond, Watermain Woods, 24.X.1981, *42529* (**Representative Specimen**), *42605, 42611, 42642–42644, 42647* (TENN). Kittitas Co., Snoqualmie National Forest, Pacific Crest Trail, Stampede Pass, 14.X.1981, *42634–42636* (TENN); Snoqualmie National Forest; near Cooper's Lake, 24.X.1981, *42645–42649, 42707, 42755* (TENN); Road to Lake Kachess, ½ mi. from Interstate 90, 8.X.1984, *G. M. Mueller 1985* (F, WTU); Stampede Pass Road, 1½ miles east of Crystal Springs Campground, 18.X.1984, *G. M. Mueller 2013* (F, WTU). Mason Co., near Sheldon, north of Mason Lake, 27.X.1981, *42610, 42650, 42651, 42653, 42654* (TENN). Pierce Co., 15.X.1984, *G. M. Mueller 2008* (F, WTU). San Juan Co., 28.X.1984, *G. M. Mueller 2020, 2021, 2027* (F, WTU). Whatmon Co., Ross National Recreation Area, Pyramid Lake Trail, 8.X.1981, *42631* (TENN); Kelceme, east of Silverton, 10.X.1981, *42632* (TENN).

Laccaria fraterna

AUSTRALIA

Vic. Port Phillip, no date, *French 1* (as *Agaricus fraternus*) (K, **Holotype** of *A. fraternus*).

UNITED STATES

California: Marin Co., Mt. Tamalpais watershed, near Fairfax, Bon Tempe, 5.XII.1984, *G. M. Mueller 2130* (WTU, F); San Francisco Co., Park Merced Shopping Center, near San Francisco State University, 4.XII.1984, *G. M. Mueller 2126* (WTU, F), San Francisco State University, 6.XII.1984, *G. M. Mueller 2146* (WTU, F).

URUGUAY

Montevideo, 1927, *2800* (MPU, **Representative Specimen** of *L. lateritia*).

ZAIRE

Ori, Nioka, V.1926, *Goossens 558* (as *Naucoria goossensiae*) (BR, **Holotype** of *N. goossensiae*).

Laccaria laccata var. *laccata*

CHILE

Valdivia, Mirador, Cordillera Pelada, 6.V.1965, *Singer 6738* (SGO, **Holotype** of *L. laccata* var. *gibba*).

CSSR

Moravia, Ostrava, Halde Lucina, 30.VIII.1968, *Veselsky s.n.* (F, **Holotype** of *L. laccata* var. *vulcanica*).

SWEDEN

Småland, Femsjö, 17.VIII.1964, *Singer C4083* (BAFC, **Neotype** of *L. laccata*); 28.IX.1959, *F. Karlvall 9142* (GB); Femsjö Parish, 25.VIII.1979, *N. Lundqvist 12298* (UPS).

Laccaria laccata var. *pallidifolia*

[Some collections of *L. ohiensis* may be buried in this list because I did not note basidiospore echinulae width at the onset of this study.]

CANADA

British Columbia: Robson River, west of Jasper, 17.X.1974, *149408* (DAOM); Alice Lake Provincial Park, 3.X.1981, *43091* (TENN).

New Brunswick: Kouchibouguac National Park, 26.VI.1978, *169727* (DAOM).

Newfoundland: 17.VIII.1887, *coll. Waghorne* (NY).

Nova Scotia: Kings Co., Kentville, Ag. Station, 27.VIII.1978, *42530, 42965* (TENN); near Scott Bay, Split Bay Trail, 28.VIII.1978, *42533* (TENN); Aylesford Lake Road, 1.IX.1978, *42539, 42971* (TENN).

Ontario: Lake Tunagami, Sand Point, 5.IX.1938, *Smith 4573* (MICH); Nipissing District, Algonquin Park, 24.VIII.1974, *152464* (DAOM).

CHILE

Valdivia, Mirador, Cordillera Pelada, 5.V.1965, *Singer M5514* (BAFC, **Holotype** of *L. laccata* var. *chilensis*), *M5515* (BAFC, **Holotype** of *L. tetraspora* var. *peladae*).

CSSR

Moravia, Jeseniky, Rejúz near Jesenik, 24.VII.1974, *Singer C5664* (F, **Holotype** of *L. laccata* var. *intermedia*); Slovakia, Skalnaté pleso, 5.IX.1974, *Singer C5878* (F, **Holotype** of *L. laccata* var. *subalpina*); Malá Studená dolina, 13.IX.1974, *Singer C6001* (F, **Holotype** of *L. laccata* var. *tatrensis*); Statn, Prirodne Reservace near Bradlo, 10.IX.1970, *Singer C5120* (F).

ENGLAND

Kent: Bedgebury, National Pine Arboretum, 20.X.1960, *Singer C3119* (BARC, **Holotype** of *L. laccata* var. *anglica*).

JAPAN

Prov. Ishikari, Napporo Forest, 17.VII.1982, *Imai 314* (SAP, **Holotype** of *L. laccata* f. *minuta*).

SWITZERLAND

Schweiz, ZH, Birmensdorf, 28.X.1965, *651338* (ZT).

UNITED STATES

Alabama: Lee Co., Auburn, 6.XII.1896, *coll. Earle* (NY).

Alaska: Little Nelchina Campground, Glenn Highway between Eagle Summit and Lake Louise Road, 13.VII.1964, *WK 1398* (TENN 43123); Chugach Mts., near Anchorage, 16.IX.1965, *WK 1406* (TENN 43124); Airport Road, near Homer, 2.IX.1967, *WK 1417* (TENN 43125); Talkeetna Junction, 4.VII.1966, *WK 1421* (TENN 42969); Anchorage, Goose Lake, 6.X.1970, *WK 4884* (TENN 42970); Girdwood, Alyeska Ski Area, 2.VII.1964, *WK 1404* (TENN 42968); Potter,

11.IX.1971, *WK 6170* (TENN 42967); Glacier Bay National Monument Headquarters, 26.IX.1978, *39146* (OSC).

Arizona: Grand Canyon National Park, North Rim, Point Sublime Road, 19.VIII.1971, *Thiers 27748* (SFSU).

California: Del Norte Co., Hwy. 199 at Oregon border, 29.X.1971, *Thiers 28490* (SFSU). Mendocino Co., Jackson State Forest, 31.X.1972, *Thiers 30413* (SFSU); same locality, 26.X.1975, *Halling 975* (SFSU); Stanford University, 4.XII.1902, *Copeland 8* (NYS). San Mateo Co., Wonderlich Co. Park, 6.XII.1984, *G. M. Mueller 2148* (F, WTU).

Colorado: Jackson Co., Colorado State Forest, Cameron Pass, 15.IX.1981, *43090* (TENN). Larimer Co., Roosevelt National Forest, Blue Lake Trail, 13.IX.1981, *43089* (TENN); San Juan Mts., Trout Lake, 16.VII.1956, *Smith 53015* (MICH); Frying Pan River, 30 miles east of Basalt, 10.VII.1979, *Thiers 40168* (SFSU).

Florida: Alachua Co., Gainesville, 5.I.1943, *coll. West* (FH); Austin Cary Memorial Forest, Lake Mize, 16.VIII.1985, *G. M. Mueller 2216–2219* (F). Marion Co., Ocala National Forest, Mill Dam Road, 24.VIII.1980, *43054–43057* (TENN); Ocala National Forest, fire road off 40, 24.VIII.1980, *43058* (TENN); Newman's Lake, Hatched Creek, 4.VII.1932, *F16196* (FLAS).

Georgia: Rabun Co., Black Rock Mountain State Park, 14.IX.1979, *43034, 43035, 43037–43041, 43043, 43044, 43046* (TENN); Rabun Bald, 23.IX.1983, *G. M. Mueller 1806, 1808, 1809* (TENN).

Idaho: Idaho Co., Selway National Forest, 30.VII.1936, *Rossbach 218* (FH).

Illinois: Jackson Co., Fountain Bluff, near Gorham, 17.VIII.1977, *Mueller 131* (SIU). Little Grand Canyon, 3.IX.1977, *Mueller 161* (SIU), *Sundberg 2374, 2594* (SIU); Giant City State Park, Devils Stand Table area, 8.VI.1981, *42962, 43081–43086* (TENN); Devils Kitchen Lake Recreation area, 9.VI.1981, *42546, 42963* (TENN). Perry Co., Pyramid State Park, 7.VI.1981, *43080* (TENN). Pope Co., Bell Smith Springs, 1.X.1977, *Mueller 259, 262, 267, 268, 270, 273, 275* (SIU); same locality, 9.V.1981, *43087, 43088* (TENN). Williamson Co., Crab Orchard Wildlife Refuge, 6.XI.1977, *Mueller 390, 393* (SIU); River Forest, 21.VII.1902, *coll. Harper* (F).

Louisiana: St. Tammany Parish, Fontainebleau State Park, 8.XII.1980, *43076* (TENN); Honey Island Nature Trail, 10.XII.1980, *43077–43079* (TENN); Walker, 31.VII.1952, *Stuntz F296, 7308a* (WASH).

Maine: Oxford Co., Canton Pt., 13.X.1942, *45856* (CUP); Penobscot Co., Old Town, College Ave., University of Maine, 13.VII.1972, *Homola 5157* (MAINE); Orono, Bangor Bog, 8.X.1974, *Kimball 6159* (MAINE); Northport, Bayside area, 8.IX.1974, *Kimball 6036* (MAINE).

Maryland: Laurel, Beltsville Forest Dis. Lab., Telegraph Road, 16.X.1969, *Miller 8228* (VPI).

Massachusetts: Berkshire Co., North Adams, 16.VIII.1986, *G. M. Mueller 2530, 2533* (F).

Michigan: Cheboygan Co., U. of Michigan Biol. Station, Hogsback Rd., 24.VIII.1984, *G. M. Mueller 1829* (F, WTU); U. of M. Biol. Station, Reeses Swamp, 5.IX.1984, *G. M. Mueller 1845, 1847, 1852* (F, WTU); same locality, 6.IX.1984, *G. M. Mueller 1862* (F, WTU); U. of M. Biol. Station, The Gorge, 6.IX.1984, *G. M. Mueller 1855, 1858* (F, WTU); south C64, near Indian Trail Rd., 6.IX.1984, *G. M. Mueller 1868, 1869* (F, WTU). Jackson Co., Sharron Hollow, 26.VI.1937, *Smith 6409* (MICH). Marquette Co., off Big Bay Rd., near Marquette, 13.IX.1984, *G. M. Mueller 1884, 1886, 1888* (F, WTU); Big Bay Rd. between Harlow Creek & Eagles Nest, 14.IX.1984, *G. M. Mueller 1907, 1908, 1910–1913* (F, WTU); Powder Mill Rd.. 15.IX.1984, *G. M. Mueller 1917, 1918* (F, WTU). Montmorency Co., 8.VII.1981, *Thiers 22213* (SFSU); Washtenaw Co., Ann Arbor, 18.VIII.1943, *Smith 18862* (TENN); Neebish, VIII.1911, *Harper 3106* (F); Hartwig Pines, 13.VIII.1957, *Stuntz 10568* (WASH).

Mississippi: Harrison Co., DeSoto National Forest, 6.XII.1980, *43075* (TENN).

New Jersey: Mammonth Co., 18.VI, *coll. Ballou* (NY); Newark, 1890, *coll. Ellis* (NY).

New York: Bronx Co., New York Botanical Garden, *Murrill s.n.* (NY). Warren Co., Boltom Landing, August, *coll. Peck* (NYS, **Holotype** of *C. laccata* var. *decurrens*); Washington Co., east of Tripoli Lake George region, 7–14.X.1918, *4415* (CUP); Menands, Piseco, 26.VIII.1928, *Peck s.n.* (NYS); Newcomb, Huntington Wild Life Forest, 6–17.IX.1941, *coll. Singer* (FH); Selkirk, Lake Mohonk, October, *coll. Peck* (NYS, **Holotype** of *C. laccata* var. *pallidifolia*).

North Carolina: Hendersonville Co., near Camp Green Cove, 14.IX.1980, *43049* (TENN); same locality, 17.IX.1980, *43060, 43061* (TENN); near Camp Green Cove, Davis Creek Trail, 15.IX.1980, *42959, 42960* (TENN); near Camp Green Cove, Scheck property, 19.IX.1980, *42961, 43061–43068* (TENN); near Camp Green Cove, 19.IX.1980, *43069* (TENN); same locality, 20.IX.1980, *43070–43074* (TENN). Jackson Co., Whiteside Mt. Trail,

16.VII.1979, *42979–42983* (TENN); same locality, 9.IX.1979, *42996–43002* (TENN); same locality, 8.VIII.1980, *42958* (TENN); same locality, 16.IX.1983, *G. M. Mueller 1736* (TENN). Macon Co., Lamb Mt. Road, 13.VII.1979, *42972–42974* (TENN); near Highlands, Chiquapin Mt. Trail, 13.VII.1979, *42975* (TENN); same locality, 18.IX.1983, *G. M. Mueller 1764, 1765* (TENN, F); Chattooga River Trail, 19.IX.1983, *G. M. Mueller 1774* (TENN); Highlands Biological Station, near Ilges Cottage, 14.VII.1979, *42976, 42977* (TENN); Elicot Rock Trail, 17.VII.1979, *42984* (TENN); Nantahala National Forest, Wayah Bald, 18.VII.1979, *42957, 42985–42991* (TENN); same locality, 11.IX.1979, *43007–43016* (TENN); Nantahala National Forest, near Highlands, off U.S. 64, 10.IX.1979, *43003, 43004* (TENN); Nantahala National Forest, Glen Falls area, 10.IX.1979, *43005, 43006* (TENN); Highlands, Ravenel Park, 12.IX.1979, *43017–43020* (TENN); near Highlands, Horse Cove, 13.IX.1979, *43021–43025* (TENN); same locality, 14.VII.1979, *42978* (TENN); Coweeta Hydrologic Research Station, 14.IX.1979, *43026–43033* (TENN); same locality, 11.VIII.1980, *43050, 43051* (TENN); same locality, 17.IX.1983, *G. M. Mueller 1751, 1755* (F). Transylvania Co., Estate of G. W. Vanderbilt, 13–24.VII.1908, *coll. Murrill & House* (NY).

Ohio: Carroll Co., near Leesville Lake, Old Scott Place, 28.IX.1979, *43047, 43048* (TENN).

Oregon: Benton Co., Corvallis, 3.XI.1981, *43109* (TENN). Lane Co., Honeyman Memorial State Park, 4.XI.1981, *43111–43116* (TENN). Lincoln Co., Siuslaw National Forest, Tricullum campground, 7.XI.1981, *73117* (TENN); South Beach State Park, 8.XI.1981, *43118* (TENN); same locality, 12.XI.1981, *42964, 43119–43121* (TENN). Tillamook Co., Camp Meriwether, 12.XI.1976, *Thiers 36956* (SFSU).

South Carolina: Oconee Co., Sumter Nation Forest, Foothills Trail, near NC state line, 20.IX.1983, *G. M. Mueller 1778, 1779, 1785, 1787* (TENN).

Tennessee: Sevier Co., Great Smoky Mountains National Park, Ramsey Cascade area, 30.VII.1979, *42992–42995* (TENN).

Texas: Orange Co., Vidor, 455 Virginia Lane, 27.XI.1985, *G. M. Mueller 2292* (F). Polk Co., Big Thicket Nature Preserve, Big Sandy Unit, 29.XI.1985, *G. M. Mueller 2307* (F). Tyler Co., Big Thicket Nature Preserve, Turkey Creek Unit, 29.XI.1985, *G. M. Mueller 2320* (F).

Utah: Wasatch National Forest, between Bald Mountain Pass and Evanston, 4.VIII.1970, *Thiers 26698* (SFSU).

Vermont: Starksboro, 2.IX.1880, *coll. Pringle* (FH); Wallingford, Elfin Lake, 6.X.1952, *38894* (CUP).

Virginia: Giles Co., Mountain Lake, 8–14.VII.1909, *coll. Murrill* (NY); Mountain Lake Biological Station, 17.VIII.1983, *G. M. Mueller 1716* (TENN).

Washington: Grays Harbor Co., Ocean City State Park, 20.X.1981, *43096–43098* (TENN); same locality, 21.X.1981, *43099–43103* (TENN). King Co., Seattle, Woodland Park, 11.X.1981, *43092, 43093* (TENN); Snoqualmie National Forest, Asahel Curtis Nature Trail, 13.X.1981, *43094* (TENN). Kittitas Co., Snoqualmie National Forest, Pacific Crest Trail, Stampede Pass, 14.X.1981, *43095* (TENN); Snoqualmie National Forest, near Cooper's Lake, 24.X.1981, *43104, 43106* (TENN). Mason Co., near Sheldon, north of Mason Lake, 27.X.1981, *43106–43108* (TENN). Pierce Co., Mt. Rainier National Park, Caibon River, 22.VII.1948, *Smith 29255* (MICH).

West Virginia: Pocahontas Co., Cranberry Backcountry, 9.IX.1981, *43126* (TENN). Randolph Co., Monongahela National Forest, Stuart Recreation Area campground, 3.VIII.1980, *43049* (TENN).

Wisconsin: Devil's Lake, VII.1911, *Harper 3397* (F).

Wyoming: Carbon Co., Medicine Bow Mts., 15.VIII.1950, *Solheim 45768* (RM).

Laccaria longipes

CANADA

Ontario: Nipissing District, Algonquin Provincial Park, Spruce Bog Trail, 18.IX.1984, *G. M. Mueller 1925–1929* (F, WTU) (*GMM 1929,* **Holotype**); same locality, *G. M. Mueller 1493, R. Singer 5159* (F).

UNITED STATES

Michigan: Iron Co., 16 km north of Iron River, 3.IX.1990, *J. J. Steinke s.n.* (F).

Minnesota: Cook Co., Grand Marais, 29.VIII.1986, *R. L. Doudrick Grand Mariais # 1* (F).

New York: Clinton Co., Hearn Swamp, under

Abies, Picea, in *Sphagnum* bog, 23.VIII.1991, *R. E. Halling 6618* (NY).

Wisconsin: Ozaukee Co., UW–Milwaukee Field Station, Sapa Spruce bog, 5.X.1989, *A. D. Parker s.n.* (F).

Laccaria maritima

CANADA

Northwest Territories: District of Keewatin, Rankin Inlet, NE shore of the Meliadine River about 5 km from the mouth, 8.VIII.1974, *E. & M. Ohenoja 8.8.1974/47a* (DAOM).

GREENLAND

Meddel. Grønland: St. Pori, Yyteri, 6.XI.1960, *P. Kallio 147/11* (UPS).

SWEDEN

Gotland: Norsta aura, 6.XI.1982, *P. Fåhraeus 1606* (UPS).

Västerbotten: Hornefors, Norrmjöle, Bettnsand, 17.IX.1980, *T. Eriksson & J. Nitare s.n.* (UME).

Laccaria montana

CANADA

British Columbia: Alice Lake Provincial Park, near Vancouver, 5.X.1981, *42885* (TENN).

DENMARK

Faeröe Islands: Ostedo, Slottorotinde, 17.VII.1938, *coll. Moller* (C, **Holotype** of *L. laccata* var. *montana*).

SWITZERLAND

Valais, Borgne de Fepecle, 11.VII.1971, *Singer 5464* (F, **Holotype** of *L. montana*).

UNITED STATES

Alaska: Navy Arctic Research Lab, USIBP Tundra Biome Sites, 4.VIII.1977, *Laursen 1172* (WTU); same locality, 26.VIII.1978, *Laursen 1397* (WTU); same locality, 28.VII.1979, *Laursen 1500* (WTU).

Colorado: Jackson Co., Colorado State Forest, Cameron Pass, 15.IX.1981, *42879–42881* (TENN). Larimer Co., Roosevelt National Forest, Blue Lake Trail, 13.IX.1981, *42877, 42878* (TENN); San Juan Mts., Trout Lake, 16.VIII.1956, *Smith 52298* (MICH).

Idaho: Bonner Co., Kaniksu National Forest, West Side Priest Lake Road, 28.IX.1981, *42882–42884* (TENN).

Montana: Avalanche Campground, 20.VII.1979, *Miller 18092* (VPI).

Washington: Clallam Co., Fort Flagler State Park, 16.X.1981, *42892* (TENN). Kittitas Co., Snoqualmie National Forest, near Kachess Lake, 14.X.1981, *42887–42891* (TENN); Wenatchee National Forest, road to Salmon La Sac, Cle Elum Lake, 26.V.1984, *G. M. Mueller 1813, 1814* (F, WTU). King Co., Snoqualmie National Forest, Asahel Curtis Nature Trail, 13.X.1981, *42886* (TENN).

Wyoming: Pole Mts., 19.VII.1950, *Smith 34945* (MICH).

Laccaria nobilis

CANADA

Nova Scotia: Kings Co., Scotts Bay, Split Cape, 28.VIII.1978, *42532* (TENN).

Ontario: Algonquin Provincial Park, 18.IX.1984, *G. M. Mueller 1932* (F, WTU).

UNITED STATES

California: Humbolt Co., 22.XI.1984, *G. M. Mueller 2086* (F, WTU).

Colorado: Jackson Co., Colorado State Forest, Cameron Pass, 15.IX.1981, *42901, 42902* (TENN). Larimer Co., near Chambers Lake, Roosevelt National Forest, 11.IX.1981, *42897* (TENN); Roosevelt National Forest, Blue Lake Trail, 12.IX.1981, *42898* (TENN); same locality, 13.IX.1981, *42527* (**Holotype**), *42893–42896, 42899, 42900* (TENN); same locality, 16.IX.1981, *42903, 42904* (TENN).

Idaho: Boundary Co., 13.VIII.1958, *Smith 60046* (MICH).

Michigan: Mackinac Co., 7.IX.1984, *G. M. Mueller 1873* (F, WTU).

New Mexico: Mountains near Santa Fe, 11.VII.1981, *Potter 282* (MICH).

New York: Newcomb, Huntington Wild Life Forest, 17.VI.1941, *coll. Singer* (FH).

Washington: Chelan Co., 9.IX.1984, *S. A. Rehner SAR-9.1* (WTU). Gray's Harbor Co., 10.X.1984, *G. M. Mueller 2048, 2061* (F, WTU). Kittitas Co., Snoqualmie National Forest, Cooper's Lake, 24.X.1981, *42905, 42906* (TENN); Swan Lake, Box Canyon, 6.X.1984, *G. M. Mueller 1981* (F, WTU).

Laccaria oblongospora

UNITED STATES

Mississippi: Harrison Co., DeSoto National Forest, Road H-6, 6.XII.1980, *42673, 42674, 42676, 42677* (TENN); DeSoto National Forest, Road H-8, 7.XII.1980, *42522* (**Holotype**), *42524, 42672, 42675, 42679–42702* (TENN).

Texas: Polk Co., Big Thicket Nature Preserve, Big Sandy Unit, 29.XI.1986, *G. M. Mueller 2310* (F).

Laccaria ochropurpurea

CANADA

Nova Scotia: Kentville, 1.IX.1950, *111857* (DAOM).

Ontario: Lake Musdoda, Creighton's Point, 28.VIII.1940, *10147* (DAOM); near Ottawa, Green's Creek, 22.VIII.1927, *40933* (DAOM); same locality, 10.IX.1928, *40931* (DAOM); St. Lawrence Island National Park, McDonald Island, *154703* (DAOM); same locality, 29.IX.1976, *158826* (DAOM).

Quebec: Mt. Burnet, 5.X.1935, *F5968* (DAOM); near Chelsea, Gilmour's Grove, 2.VIII.1923, *40932* DAOM).

UNITED STATES

Alabama: Montgomery, Johnson Woods, 4.X.1942, *coll. Burke* (MICH); Montgomery, *coll. Burke* (NY).

Florida: Planera Hammock, 3.I.1939, *19516* (FLAS).

Illinois: Alexander Co., *West 887, 896* (SIU). Jackson Co., *Burton 156* (SIU); Little Grand Canyon, 3.IX.1977, *Mueller 158, 159* (SIU); Giant City State Park, near Devils Stand Table, 9.IX.1977, *Mueller 179–182, 185* (SIU); Lake Murphysboro, 2.X.1977, *Mueller 307* (SIU); Giant City State Park, Devils Stand Table trail, 5.X.1977, *Mueller 311, 312, 314, 315* (SIU), *Sundberg 2576, 2871, 2876, 2936* (SIU). Perry Co., Pyramid State Park, near Heron Pond, 16.X.1977, *Mueller 367* (SIU). Union Co., *West 819, 842, 937* (SIU). Williamson Co., *Jones 136* (SIU); near Devils Kitchen Lake, 24.X.1977, *Mueller 238* (SIU); near Little Grassy Lake, 5.X.1977, *Mueller 320* (SIU), *Sundberg 2956* (SIU); Glencoe, X.1909, *Harper 2640* (F); Glen Ellen, X.1902, *coll. Harper* (F).

Iowa: Iowa City, 12.IX.1938, *33863* (CUP).

Kentucky: Middlesboro, 1.X.1914 (NY).

Maine: Penobscot Co., Old Town, Country Road, 20.VIII.1971, *Homola 5018* (MAINE).

Maryland: Baltimore Co., Gunpowder Region, 27.IX.1919, *Kelly 207* (FH); Laurel, 6.IX.1965, *Miller 3532* (VPI).

North Carolina: Haywood Co., Great Smoky Mountains National Park, Big Creek area, 27.IX.1979, *42911, 42912* (TENN). Hendersonville Co., near Camp Green Cove, 13.IX.1980, *42908, 42913, 42914* (TENN); same locality, 17.IX.1980, *42915–42917* (TENN); same locality, 19.IX.1980, *42909, 42918* (TENN). Transylvania Co., Piscah National Forest, Davidson Creek campground, 7.IX.1980, *42907* (TENN).

Ohio: Carroll Co., Air Strip Trail area, 29.IX.1979, *42910* (TENN). Highland Co., Fort Hill, 14.X.1961, *Cooke 32898* (MICH); Cincinnati, *Lea 261* (K, **Holotype**).

Pennsylvania: Warren Co., near Brookston Tronesta Tract, 25.VII.1940, *Henry 3878* (FH).

South Carolina: Near Charleston, Folly Island, 16.II.1916, *coll. Small & Bragg* (NY).

Texas: Houston, 14.I.1942, *coll. Fisher* (F); *8140* (CUP).

Vermont: Lamoille Co., near Mt. Mansfield, Ranch Brook, 27.VII.1964, *Bigelow 13088* (MASS); Dummerston, Dutton Pines, 23.IX.1961, *Bigelow 9843* (MASS). Orleans Co., Greensboro, on the approach to L. B. Smith's Caspian Lake house, 20.VIII.1986, *E. O. Farwell 5074* (F).

Virginia: Giles Co., Mountain Lake, 2–4.IX.1936, *coll. Linder* (FH); Near Mountain Lake, White Pine Lodge, VIII.1947, *coll. Wilson* (FH). Grayson Co., Jefferson National Forest, Lewis Fork Trail, 9.IX.1981, *43127* (TENN).

West Virginia: Cabell Co., Huntington, Enslow Addition, 6.X.1938, *coll. Balser* (FH). Greenbrier Co., 12.IX.1980, *43128* (TENN).

Wisconsin: Lodi, 1.X.1977, *166267* (DAOM); 8.IX.1939, *coll. Olmsted* (F).

Laccaria ohiensis

ARGENTINA

Neuquen: Parque Nacional de Nahuel Huapi, Camino a los Cántaros, 14.III.1959, *Singer M1774* (BAFC, **Holotype** of *L. tetraspora* var. *aberrans*).

Rio Negro: Bahía López, 22.XI.1964, *Singer M4063* (BAFC, **Representative Specimen** of *L. tetraspora* var. *xena*).

CHILE

Peulla: Todos los Santos, 22.III.1959, *Singer M1991* (BAFC, **Holotype** of *L. tetraspora* var. *peullensis*); Valdivia, Cordillera Pelada, 28.III.1963, *Singer M3191* (BAFC, **Holotype** of *L. tetraspora* var. *valdiviensis*).

SCOTLAND

Lake Katrim, 1.VIII.1964, *Singer C4002* (BAFC, **Holotype** of *L. tetraspora* var. *scotica*).

SWEDEN

Uppland: Little Rolby, 18.IX.1982, *G. M. Mueller 1505* (UPS); Uppsala, near Hågaby, 25.X.1982, *G. M. Mueller 1604* (UPS).

UNITED STATES

Florida: Highland Co., Highland Hammock State Park, 11.VIII.1942, *Singer F160* (FH, **Holotype** of *L. tetraspora*).

Louisiana: East Baton Rouge Parish, Burden Farm, Essen Road and I-10, 3.XII.1985, *G. M. Mueller 2354* (F).

New York: Bronx Co., New York Botanical Garden, 13.VIII.1902, *coll. Earle* (NYS, **Holotype** of *C. tortilis* var. *gracilis*).

Ohio: Columbus, *Sullivant s.n.* (NY, **Holotype** of *A. ohiensis*).

West Virginia: Monroe Co., Jefferson National Forest, White Rocks Campground, The Virginias Forest Walk, 19.VIII.1983, *G. M. Mueller 1730* (TENN).

Laccaria proxima

CANADA

British Columbia: Alice Lake Provincial Park, 3.X.1981, *42942* (TENN); Garibaldi Provincial Park, 5.X.1981, *42945–42947* (TENN).

Nova Scotia: Kings Co., near Scotts Bay, Split Bay Trail, 28.VIII.1978, *42537* (TENN).

FRANCE

Montmorency, Chestnut Hill, 20.X.1903, *coll. Atkinson* (CUP); Montmorency, XI.1904, *coll. Boudier* (PC, **Representative Specimen**); St. Die Vosges, 21.VIII.1910, *coll. Atkinson, 24995* (CUP).

ITALY

Trento, X.1899, *Bresadola s.n.* (NY).

SWEDEN

Uppland: Uppsala, Stadsskogen, 19.IX.1982, *G. M. Mueller 1518* (UPS).

UNITED STATES

Alaska: Point Barrow, Navy Arctic Research Lab, I.B.P. site, 3.VII.1971, *WK 4573* (TENN 42928); Arctic Valley, 31.VIII.1971, *WK 540A* (TENN 42929); NARL, USIBP Tundra Biome Site 3, 28.III.1979, *Laursen 1499* (WTU).

California: Marin Co., Mt. Tamalpais water shed, near Fairfax, Bon Tempe, 5.XII.1984, *G. M. Mueller 2131* (F, WTU). Yuba Co., Bullards Bar Rec. Area, 30.XI.1984, *G. M. Mueller 2100* (F, WTU).

Colorado: Jackson Co., Colorado State Forest, Cameron Pass, 15.IX.1981, *42875, 42876* (TENN).

Florida: Alachua Co., Gainesville, 29.XII.1942, *F1672* (FLAS); same locality, 1.I.1949, *F45770* (FLAS). Marion Co., Ocala National Forest, near

Mill Dam Road, 24.VIII.1980, *42939* (TENN). Sarasota Co., Sarasota, XII.1980, *Williams 1000* (TENN); same locality, 16.XII.1981, *Williams 1006* (TENN).

Idaho: Bonner Co., Kaniksu National Forest, Binarch Creek Road, 26.IX.1981, *42920* (TENN); same locality, 27.IX.1981, *42921, 42943* (TENN); Kaniksu National Forest, 27.IX.1981, *42944* (TENN); Kaniksu National Forest, West Side, Priest Lake Road, 28.IX.1981, *42922* (TENN).

Michigan: Washtenaw Co., Whitmore Lake, 4.IX.1977, *Smith 87798* (MICH).

Mississippi: Harrison Co., DeSoto National Forest, Airey Lake, 6.XII.1980, *42940, 42941* (TENN).

North Carolina: Hendersonville Co., Camp Green Cove, 20.IX.1980, *42873, 42874* (TENN). Jackson Co., Whiteside Mountain, 9.IX.1979, *42030–42032, 42919* (TENN). Macon Co., Nantahala National Forest, Wayah Bald, 11.IX.1979, *42933, 42934* (TENN); near Highlands, Horse Cove, 13.IX.1979, *42935* (TENN).

Ohio: Carroll Co., Air Strip Trail area, 29.IX.1979, *42936–42938* (TENN).

Oregon: Benton Co., Corvallis, Oregon State University campus, 2.XI.1981, *42951* (TENN). Lincoln Co., Siuslaw National Forest, Trillicum campground, 8.XI.1981, *42952* (TENN); South Beach State Park, 12.XI.1981, *42927, 42953* (TENN). Tillamook Co., Meriwether Dunes, 13.XI.1981, *42954* (TENN); Southside Sand Lake, 20.XI.1978, *Hunt 027* (OSC).

Washington: King Co., Snoqualmie National Forest, Asahel Curtis Nature Trail, 13.X.1981, *42923* (TENN); near Redmond, Watermain Woods, 24.X.1981, *42924* (TENN). Kittitas Co., Snoqualmie National Forest, near Cooper's Lake, 24.IX.1981, *42925* (TENN). Mason Co., near Sheldon, north of Mason Lake, 27.X.1981, *42926, 42949, 42950* (TENN). Whatcom Co., Ross National Recreation Area, Pyramid Lake Trail, 8.X.1981, *42948* (TENN).

Laccaria pumila

CANADA

Nova Scotia: Kings Co., near Scotts Bay, Split Bay Trail, 28.VIII.1978, *42531* (TENN); Alysford Lake Road, 1.XI.1982, *42541, 42550* (TENN).

FRANCE

Dept. Alpes Maritimes: Col de la Cayolle, 18.VII.1976, *J. Trimbach 1453* (L, **Neotype** of *L. pumila*).

UNITED STATES

Alaska: Barrow, between Elson Lagoon and Oil Well Road, 5.VII.1970, *WK 4609* (TENN 43122); Fairbanks, Peger Road, 17.VIII.1981, *WK 5323* (TENN 42551); Steese Highway (110 miles north of Fairbanks), Eagle Summit, 19.VIII.1971, *WK 5355* (TENN 42549); NARL, USIBP Tundra Biome Site 1, 26.VIII.1978, *Laursen 1398* (WTU); Delong Mountains, Driftwood Camp, 2.X.1978, *Laursen 1424* (WTU).

Colorado: Larimer Co., Rocky Mountain National Park, Bear Lake Road, 20.VII.1940, *Mains 5115* (MICH); Roosevelt National Forest, near Chambers Lake, 11.IX.1981, *42548* (TENN); Roosevelt National Forest, Blue Lake Trail, 13.IX.1981, *42547, 42552, 42554–42558* (TENN); same locality, 16.IX.1981, *42553* (TENN).

Michigan: Cheboygan Co., Mud Lake Bog, 13.X.1934, *Smith 1150* (MICH).

Washington: Clallam Co., Olympic Peninsula, Fort Flagler State Park, 16.X.1981, *42562* (TENN). Kittitas Co., Snoqualmie National Forest, near Kachess Lake, 14.X.1981, *42559–42562* (TENN); same locality, 4.X.1984, *G. M. Mueller 1956* (F, WTU).

Wyoming: Medicine Bow Mountains, 8.IX.1923, *coll. Kauffman* (MICH).

USSR

Kuraika, 31.VII.1937, *Singer A439* (as *L. altaica*) (LE, **Holotype** of *L. altaica*).

Laccaria striatula

CANADA

Nova Scotia: Kings Co., Baxter Harbor, 31.VIII.1978, *42534, 42536, 42767* (TENN); Aylesford Lake Road, 1.IX.1978, *42538, 42540, 42542, 42543, 42768, 42769, 42773* (TENN); Cape Split, Split Bay Trail, 1.IX.1978, *42776* (TENN).

Ontario: Nipissing District, Algonquin Provincial Park, Beaver Pond Trail, 19.IX.1984, *G. M. Mueller 1940* (F, WTU), Spruce Bog Trail, 21.IX.1984, *G. M. Mueller 1944* (F, WTU).

UNITED STATES

Georgia: Rabun Co., Rabun Bald, 12.VIII.1980, *42849, 42850* (TENN).

Michigan: Cheboygan Co., University of Michigan Biological Station, 11.VII.1961, *Charlton G36* (MICH); Neebish, IX.1916, *coll. Harper* (F). Marquette Co., 14.IX.1984, *G. M. Mueller 1909* (F, WTU).

New York: Catskill Mountains, September, *C. H. Peck s.n.* (NYS, **Holotype** of *L. laccata* var. *striatula*). Lake Piseco, VIII.1902, *14726* (CUP).

North Carolina: Hendersonville Co., near Camp Green Cove, 14.IX.1980, *42865* (TENN); same locality, 17.IX.1980, *42770–42772* (TENN); same locality, 19.IX.1980, *42866, 42871* (TENN). Jackson Co., Whiteside Mt. Trail, 16.VII.1979, *42762, 42777–42779* (TENN); same locality, 9.IX.1979, *42798–42817* (TENN); same locality, 8.VIII.1980, *42838–42840* (TENN); same locality, 13.VIII.1980, *42852–42859* (TENN). Macon Co., Elicot Rock Trail, 18.VII.1979, *42774, 42775, 42780* (TENN); Nantahala National Forest, Wayah Bald, 11.IX.1979, *42818–42831* (TENN); same locality, 9.VIII.1980, *42841–42846* (TENN); Ravenel Park, 12.IX.1979, *42832* (TENN); Coweeta Hydrologic Research Station, 14.IX.1979, *42833–42837* (TENN); same locality, 11.VIII.1980, *42847, 42848* (TENN); Nantahala National Forest, Glen Falls, 13.VIII.1980, *42851* (TENN).

South Carolina: Oconee Co., 20.IX.1983, *G. M. Mueller 1780* (TENN).

Tennessee: Blount Co., Great Smoky Mountains National Park (= GSMNP), Cades Cove, Parsons Branch Road, 28.IX.1980, *42867, 42868* (TENN). Carter Co., Cherokee National Forest, Roane Mt., 11.X.1980, *42869–42872* (TENN). Sevier Co., GSMNP, Mt. LeConte, 19.VI.1938 (FH); GSMNP, Ramsey Cascade area, 31.VII.1979, *42781* (TENN); GSMNP, Clingman's Dome, 1.IX.1979, *42761, 42783–42797* (TENN); same locality, 6.IX.1980, *42860–42865* (TENN); GSMNP, Alum Cave Trail, 10.VII.1981, *42763, 42765* (TENN).

Laccaria tortilis

ARGENTINA

La Baea, V.1880, *Spegazzini 2891* (LPS, **Holotype** of *A.* [*Clitocybe*] *echinosporus*).

CANADA

Ontario: Grenadier Island, St. Lawrence Island National Park, 10.VII.1975, *Redhead 1619* (DAOM); Leeward Island, St. Lawrence National Park, 22.VII.1976, *159029* (DAOM).

SCOTLAND

Yorkshire, Tanfield Lodge, 6.IX.1969, *Orton 3642* (E, **Representative Specimen**); Island of Mull, near Quinish House, 7.IX.1976, *Watling 12479* (E); Norfolk, Surlingham Wood, 25.VIII.1969, *Orton 3641* (E); Perthshire, 17.VIII.1972, *Watling 9465* (E), Perthshire, Inver, 27.X.1975, *Watling 11347* (E); Yorkshire, Bishop Wood, 26.IX.1971, *Watling 8947* (E).

UNITED STATES

Illinois: Cook Co., Harms Woods Forest Preserve, 2.VIII.1990, *G. M. Mueller 4061* (F).

Maine: Penobscot Co., Orono, Bangor Bog, 8.X.1974, *Homola 6158* (MAINE); Newburgh, Bog Brook area, 15.IX.1974, *Kimball 6078* (MAINE).

Massachusetts: Hamilton Co., Amherst, Sunset Ave., 16.V.1976, *Baroni 2445* (MASS).

Michigan: Cheboygan Co., Burt Lake, Colonial Point, 1.X.1960, *Smith 63093* (MICH); Colonial Point, 6.IX.1969, *Ammirati 3845* (MICH); Marquette, 4.IX.1933, *Smith 33862* (MICH); Neebish, VIII.1909, *Harper 2372* (F); Neebish, IX.1917, *coll. Harper* (F).

New York: Sand Lake, August, *coll. Peck* (NYS).

North Carolina: Giles Co., Mt. Lake Biological Station, Rhododendron trail, 17.VIII.1983, *G. M. Mueller 1710* (TENN).

Oregon: Benton Co., Corvallis, Oregon State University, 2.XI.1981, *42955* (TENN).

Washington: *Smith 14296* (MICH). Whatcom Co., Bellingham, VIII.1978, *B. McAdoo 78#28* (F).

Wyoming: NE Pole Mt. area, 7.VIII.1950, *Smith 34564* (MICH).

THE NETHERLANDS

Noord-Brabant, Ulvenhout near Breda, 18.VIII.1959, *Maas Geesteranus 12908* (MICH).

Laccaria trichodermophora

UNITED STATES

Alabama: Montgomery, *coll. Burke* (NY).

Illinois: Alexander Co., *West 878, 889* (SIU). Pope Co., Bell Smith Springs Recreation Area, 1.X.1977, *Mueller 257* (SIU). Union Co., Union Co. Forest Reserve, 30.X.1977, *Mueller 388* (SIU), *West 931* (SIU). Williamson Co., Crab Orchard Wildlife Refuge, 6.X.1977, *Mueller 394* (SIU).

Louisiana: St. Tammany Parish, Fontainebleau State Park, 8.XII.1980, *42722–42725* (TENN); Honey Island Nature Trail, 10.XI.1980, *42732* (TENN); 1.X.1985, *G. M. Mueller 2329* (F). Tangipahoa Parish, Chappepeela Creek, 5.VI.1976, *Bigelow 17668* (TENN).

Mississippi: Hancock Co., NASA Test Site, 9.XII.1980, *42730, 42731* (TENN). Harrison Co., DeSoto National Forest, Road H-6, 5.XII.1980, *42523* (**Holotype**), *42703–42705, 42708–42711, 42733* (TENN); same locality, 6.XII.1980, *42716–42718* (TENN); DeSoto National Forest, near Airey Lake, 6.XII.1980, *42706, 42719* (TENN); DeSoto National Forest, trail to P.O.W. Camp, 6.XI.1980, *42712–42715* (TENN); DeSoto National Forest, near Harrison Experimental Forest Office, 7.XII.1980, *42720, 42721* (TENN). Pearl River Co., Picayune, woods behind Bill Cibula's home, 9.XII.1980, *42726–42729* (TENN). Perry Co., 6.X.1985, *G. M. Mueller 2372* (F).

North Carolina: Hendersonville Co., near Camp Green Cove, Davis Creek Trail, 17.IX.1980, *42752* (TENN); Scheck Property, 19.IX.1980, *42753* (TENN). Jackson Co., Whiteside Mt., 16.IX.1983, *44153* (TENN). Macon Co., Highlands, Ravenel Park, 12.IX.1979, *42756* (TENN); Nantahala National Forest, Chattooga River Trail, 19.IX.1983, *44165, 44167* (TENN); Nantahala National Forest, Wayah Bald, 22.IX.1983, *G. M. Mueller 1804* (F).

South Carolina: Oconee Co., Sumter National Forest, Foothills Trail, 20.IX.1983, *44169, 44173* (TENN).

Tennessee: Knox Co., I. C. King Park, 7.VI.1979, *42760* (TENN). Sevier Co., Great Smoky Mountains National Park, Clingman's Dome, 6.IX.1980, *42521, 42754, 42758, 42759* (TENN).

Texas: Hardin Co., 26.XI.1985, *G. M. Mueller 2282, 2283* (F). Polk Co., 29.XI.1985, *G. M. Mueller 2306, 2308* (F). Tyler Co., 29.XI.1985, *G. M. Mueller 2315, 2319, 2321, 2324, 2325* (F).

West Virginia: Tucker Co., Blackwater Falls area, 4.VIII.1980, *M2757* (TENN).

Laccaria trullissata

CANADA

New Brunswick: Kouchibouguac National Park, 3.X.1978, *169941* (DAOM); Kouchibouguac National Park, Kelly's Beach, 7.IX.1978, *169582* (DAOM).

UNITED STATES

Connecticut: Deep River, Cockaponsett State Park, 18.IX.1966, *coll. Lucas* (MASS).

Florida: Levy Co., Cedar Keys, Way Key, 22.I.1949 (F). Okaloosa Co., Fort Walton Beach, 1.XII.1985, *G. M. Mueller 2352* (F).

Illinois: Peoria, IX.1969, *coll. Grundy* (MASS).

Indiana: Deaverly Shores, *Singer N1815* (F).

Maine: Oxford Co., near Brownfield, 28.X.1973, *Homola 5879* (MAINE).

Maryland: Talbot Co., Choptemk River, 24.IX.1922, *coll. Fisher* (MICH); Hoffman Hill Road, Beltsville Exp. Forest, 6.XI.1968, *Miller 7109* (VPI); Laurel, Beltsville Exp. Forest, 12.IX.1969, *Miller 8071* (VPI); same locality, 14.X.1969, *Miller 8225* (VPI).

Massachusetts: Franklin Co., Sunderland, 24.IX.1957, *Bigelow 6314* (MASS), *82782* (DAOM); Montague Center, 4.X.1966, *Bigelow 14916* (MASS); Cape Cod, near Marson's Mill, 26.VIII.1945, *coll. Linder* (FH); Westport, Horseneck Beach, 27.X.1973, *Bigelow 17299* (MASS).

Michigan: Baraga Co., near mouth of Huron River, 16.X.1970, *Ammirati 5687* (MICH); L'Anse, Ford Forestry Center, 19.IX.1987, *G. M. Mueller 3048* (F). Chippewa Co., Whitefish Point, 9.IX.1951, *Smith 33574* (MICH). Marquette Co., Gordon Flats, off M28, near Marquette, 14.IX.1984, *G. M. Mueller 1914* (F, WTU). Muskegon Co., Cedar Creek Twp., S.E. corner sect. 31, 16.IX.1979, *coll. Reznicek & Keddy* (MICH).

Mississippi: Jackson Co., Horn Island, 5.XII.1985, *G. M. Mueller 2360, 2361, 2363* (F).

New Jersey: Newfield, before 1874, *coll. Ellis* (NYS, **Lectotype**); Seaside Park, 29.VIII.1902, *Harshberger* (NYS); Browns Mills, 29.IX.1945, *coll. Aide*; North American fungi *101* (NY, NYS, CUP).

New York: Albany Co., Karner, 14.X.1917, *coll. House* (NYS). Suffolk Co., Wading River, VIII.1905, *coll. Peck* (NYS); Orient Point, 13.XI.1911, *coll. Latham* (CUP); Long Island, 30.IX.1956, *coll. Wetzel* (NY).

North Carolina: Bogue, 31.X.1977, *Randall 106* (NCSC).

Pennsylvania: Philadelphia, *Coll. Phettaas* (FH).

Wisconsin: Trempealoa Co., near Osseo, 18.IX.1977, *Mueller 127* (SIU).

Laccaria vinaceobrunnea

UNITED STATES

Louisiana: East Baton Rouge Parish, Burden Farm, 3.XII.1985, *G. M. Mueller 2355–2357* (F). St. Tammany Parish, Fontainebleau State Park, 8.XII.1980, *42736–42748, 42751* (TENN); same locality, 9.XII.1980, *42525* (**Holotype**), *42735, 42739* (TENN); same locality, 1.XII.1985, *G. M. Mueller 2334–2341* (F); Honey Island Nature Tail, 10.XII.1980, *42749, 42750* (TENN).

Mississippi: Hancock Co., Pass Christian, 28.XII.1972, *Smith 17772* (MICH). Harrison Co., Harrison Experimental Forest, 2.XII.1985, *G. M. Mueller 2349* (F).

Texas: Orange Co., Vidor, 455 Virginia Lane, 27.XI.1985, *G. M. Mueller 2290, 2291* (F). Polk Co., Big Thicket Nature Reserve, Big Sandy Unit, 29.XI.1985, *G. M. Mueller 2309* (F).

Appendix B. Isolates Used in Somatic Culture Mat Analyses[1]

Laccaria amethysteo-occidentalis

GMM 1256 (TENN 42526)

Laccaria bicolor

GMM 1225 (TENN 42607); GMM 1230 (TENN 42608); GMM 1264 (TENN 42604); GMM 1293 (TENN 42606); GMM 1352 (TENN 42529); GMM 1353 (TENN 42605); GMM 1478 (TENN 42603); Hunt 018 (Oregon State University culture S-447); Trappe 4755 (OSU S-282); Trappe 4779 (OSU S-283)

Laccaria laccata var. *pallidifolia*

GMM 936 (TENN 42958); GMM 975 (TENN 43055); GMM 979 (TENN 43058); GMM 1010 (TENN 42959); GMM 1011 (TENN 42960); GMM 1030 (TENN 42961); GMM 1160 (TENN 42962); GMM 1167 (TENN 42963); GMM 1168 (TENN 42546); GMM 1470 (TENN 42964); Hunt 013 (OSU S-443)

Laccaria longipes

GMM 1929

Laccaria nobilis

GMM 1198 (TENN 42527); GMM 1205 (TENN 42893)

Laccaria oblongospora

GMM 1075 (TENN 42673); GMM 1080 (TENN 42674); GMM 1100 (TENN 42675); GMM 1102 (TENN 42522); GMM 1105 (TENN 42672)

Laccaria ochropurpurea

GMM 1004 (TENN 42907); GMM 1005 (TENN 42908); GMM 1037 (TENN 42909)

Laccaria proxima

GMM 1518; 1368 (TENN 42925); GMM 2100; GMM 2131

Laccaria trichodermophora

GMM 993 (TENN 42521); GMM 994 (TENN 42754); GMM 1014 (TENN 42752); GMM 1024 (TENN 42753); GMM 1060 (TENN 42703); GMM 1063 (TENN 42733); GMM 1067 (TENN 42705); GMM 1071 (TENN 42706)

[1] Cultures are housed in the mycological culture collection at Field Museum of Natural History under the GMM number. Voucher specimens housed at TENN are filed under the TENN number.

Subject Index

Index to Taxa

Accepted names are in **boldface**, all other names are in *italics*. *Italic* page numbers designate descriptions and/or illustrations. Names mentioned incidentally are not included in this index.